PHOTO IDENTIFICATION, SUMMER ACTIVITY PATTERN, ESTIMATED FIELD METABOLIC RATE AND TERRITORY QUALITY OF ADULT MALE SEA OTTERS *(Enhydra Lutris)* IN SIMPSON BAY, PRINCE WILLIAM SOUND, ALASKA

A Dissertation

by

SHANNON ELIZABETH FINERTY

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

May 2010

Major Subject: Wildlife and Fisheries Sciences

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Approved by:

Chair of Committee,	Randall W. Davis
Committee Members,	Douglas Biggs
	Christopher Marshall
	William H. Neill
Head of Department,	Thomas E. Lacher

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ABSTRACT

Photo Identification, Summer Activity Pattern, Estimated Field Metabolic Rate and Territory Quality of Adult Male Sea Otters (Enhydra lutris) in Simpson Bay, Prince William Sound, Alaska. (May 2010)

Shannon Elizabeth Finerty, B.S., Saint Joseph's College

Chair of Advisory Committee: Dr. Randall W. Davis

This project describes a portion of a long-term study of the behavioral ecology of sea otters. Sub-studies of this project include the development of an individual recognition program for sea otters, the construction of male sea otter activity and energy budgets, and the assessment of male sea otter territory quality.

The Sea Otter Nose Matching Program, or '*SONMaP*', was developed to identify individual sea otters in Simpson Bay, Prince William Sound, Alaska, using a blotch-pattern recognition algorithm based on the shape and location of nose scars. The performance of the *SONMaP* program was tested using images of otters collected during the 2002-03 field seasons, and previously matched by visually comparing every image in a catalog of 1,638 animals. In 48.9% of the visually matched images, the program accurately selected the correct image in the first 10% of the catalog.

Individual follows and instantaneous sampling were used during the summers of 2004-06, to observe male sea otter behavior. Six behaviors (foraging, grooming, interacting with other otters, patrolling, resting, and surface swimming) were observed during four time periods (dawn, day, dusk, night) to create 24-hr activity budgets. Male sea otters spent 27% of their time resting, 26% swimming, 19% grooming, 14% foraging, 9% patrolling and 5% interacting with other otters. Field Metabolic Rate (FMR) was estimated by combining the energetic costs for foraging, grooming, resting, and swimming behaviors of captive otters from Yeates et al. (2007) with these activity budgets. 'Swimming' accounted for the greatest percentage (43%) of energy expended each day followed by grooming (23%), resting (15%), feeding (13%) and other (5%). With a peak summer sea otter density of 5.6 otters km^{-2}, the low percentage of time spent foraging indicates that Simpson Bay is below equilibrium density.

Territory quality was assessed for male sea otters using four attributes: territory size, shoreline enclosure, accessibility, and number of females observed feeding in each territory. Each attribute was coded with a score of 0-2, and total quality scores ranged from 0.14-1.96 (0.9 $\pm$ 0.61 SD). High quality territories had large areas, moderate shoreline enclosure, high accessibility, and many foraging females.

DEDICATION

For my family

ACKNOWLEDGEMENTS

I would like to thank the following people for helping to make this dissertation possible: Randall Davis for serving as the chair of my committee; Chris Marshall, Douglas Biggs and William Neil for serving on my committee and advising on various aspects of this project; Fred Weltz for logistical support in the field; the Earthwatch Institute and Texas A&M University for funding this project; the U.S. Fish and Wildlife Service for providing the permits necessary to conduct this research; Dr. Fran Gelwick for assisting with the statistical analysis, and all her patience in doing so; Heidi Pearson for consulting on statistical and GIS analysis; Erin Seney for consulting on GIS analysis; Holly (Briggs) Morin, Ian Davis, Olivia Lee, Yoko Mitani, Ryan Wolt, and Tray Wright for assistance with data collection; all of the Earthwatch volunteers and Texas A&M undergraduate class participants for their help with data collection; Felix Arnold, Stacie Arms, Jennifer Baker, Paula Canton and Dave Wentling for assisting with on-campus logistics.

Two hurricanes passed through Galveston while I researched and wrote this dissertation. I would like to extend very special thanks to my Uncle Mike and Aunt Karen Fitzgerald for sheltering me during Hurricane Rita, as well as Vernon and Geneva Parker, and the entire Parker family, for sheltering me during Hurricane Ike. I also thank Stephanie Matlock for allowing me to stay with her during my commutes to College Station after Hurricane Ike.

I would like to thank Otis Parker for all his patience and support; Jess Beck, Erin Diener, Todd Engle, Tové Goldson, Dave Hicks, Allyson Hindle, Randy Hoffman, Caleb Kopczyk, Jessie McNabb, Bridget Maloney, Ann O'Donnell and Bryan Smouther for their outside perspectives, their shoulders to cry on, and most importantly for the all the pints they shared with me (be they ice cream or alcohol).

Last, but far from least, I would like to thank my parents, John and Mary Finerty, for never letting me believe there was something I could not do, and my brothers, Patrick, Christopher, Kevin and their families for all their love and support.

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CHAPTER I

INTRODUCTION

Sea otters (*Enhydra lutris*; Order Carnivora, Family Mustelidae) are the sole species in the genus *Enhydra*. They occur in the nearshore waters of the Pacific Rim from Baja California to Japan, although there are areas in this range without sea otters (e.g., parts of northern California and Oregon). Three allopatric subspecies have been recognized: *Enhydra lutris lutris* ranges from northern Japan to the Commander Islands; *Enhydra lutris kenyoni* ranges from the Aleutian Islands east to Prince William Sound and south to Oregon; and *Enhydra lutris nereis* occurs from northern California south to Punta Abreojoa in Baja California (Riedman and Estes 1990, Reeves et al. 2002, Gilkenson 2004).

Morphology

The second-largest mustelid, exceeded in size (body length) only by the endangered giant Amazonian otter (*Pteronura brasiliensis*), and the smallest marine mammal, the sea otter represents 1 of 12 species of otters that are distributed throughout the world (Riedman and Estes 1990). An adult sea otter can weigh between 16-45 kg and is 1.2-1.5 m long. Adult males are 34% heavier and 8% longer than adult females. The head and neck of a male are heavier and more muscular than those of a female (Kenyon 1969, Riedman and Estes 1990). Other key descriptive physical characteristics include a dense fur coat covering the entire body, an elongated fifth digit on flattened hind feet

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This dissertation follows the style of Marine Mammal Science.

(flippers), retractile claws on the forepaws, a loose flap of skin under each foreleg which is used to store and transport food items, flattened molars for crushing hard-shelled macroinvertebrates, and a dorso-ventrally flattened tail (Kenyon 1969, Estes 1980, Reeves et al. 2002, Gilkenson 2004).

Aquatic Adaptations

Marine mammals exhibit similar adaptations associated with living in an aquatic environment. Having evolved many millions of years earlier, the cetaceans, pinnipeds, and sirenians are more specialized for an aquatic existence. Although the sea otter's evolutionary origins are not as ancient, it is highly adapted for life in the marine environment. The fifth digit of the hindlimbs is elongated and all of the digits are webbed to create an efficient propulsive surface (i.e., a flipper). The loosely articulated skeleton and lack of a clavicle provide the flexibility necessary for grooming and movement in water. With the hind flippers extended posteriorly, dorsoventral undulations of the entire body are used for rapid aquatic motion (Riedman and Estes 1990, Gilkenson 2004). The lung volume of a sea otter is larger than the allometric prediction for a terrestrial mammal of similar size and the lung is used as an oxygen store during diving and for buoyancy regulation at the surface (Denison and Kooyman 1973). Sea otter eyes are well adapted for both aerial and underwater vision. Like pinnipeds, the sea otter has a well developed tapetum lucidum that enhances low light vision at the surface and at depth (Reidman and Estes 1990, Gilkenson 2004). In contrast to pinnipeds, which have reduced olfactory

sensitivity, sea otters have well developed nasal turbinates and acute olfactory sensitivity. But unlike cetaceans and pinnipeds, sea otters exhibit no cranial modifications for directional sound perception underwater (Riedman and Estes 1990, Gilkenson 2004).

Habitat

Sea otters typically inhabit shallow coastal waters with both rocky and soft-sediment (sand and mud) substrates. They seldom range more than 1-2 km from shore or to depths greater than 40 m (Kenyon 1969, Riedman and Estes 1990, Gilkenson 2004) but are capable of traveling long distances across open water. Areas with canopy-forming kelp are often used by sea otters for resting and foraging, although it is not an essential habitat requirement, as several populations inhabit areas devoid of canopy-forming kelp and rest in open water (Miller 1974, Riedman and Estes 1990).

In their role as an upper trophic level predator, sea otters can have a strong top-down influence on populations of many species of benthic invertebrates. With a daily rate of food consumption equivalent to ca. 25% of their body mass (Riedman and Estes 1990), sea otters are capable of severely reducing invertebrate populations. Otters will generally select the largest prey items first, causing major declines in the populations of many commercially valuable invertebrates such as abalone, crabs, mussels and sea urchins (Kvitek and Oliver 1988, Riedmen and Estes 1990). In kelp communities, sea otter

predation on sea urchins allows the kelp to flourish and creates habitat for many other species (Duggins 1980).

Behavior

Sea otters exhibit a number of distinctive behaviors that are easily recognizable. One of these is grooming the fur, which is essential to maintain an insulating air layer next to the skin. Sea otters have the densest (up to 164,000 hairs cm^2) fur of any mammal. Each hair follicle contains up to 100 underhairs and one large guard hair (Kenyon 1969). Grooming is a behavior recognized by the repeated rubbing or stroking of the sea otter's own body using either the forepaws or the hind flippers and blowing air into the fur. The rubbing motion entwines or felts the underhairs which prevents water from penetrating the tiny interstices due to the hydrophobic surface of the hair and the surface tension properties of water. This results in an air layer within the fur, and adjacent to the skin which reduces conductive and convective heat loss. Grooming varies in intensity and is directed to every part of the otters body (Packard and Ribic 1982). Bouts of grooming are relatively short and generally occur before and after feeding and resting periods (Riedman and Estes 1990, Gilkenson 2004).

Interactive behavior occurs when two or more sea otters come into contact. This includes copulatory behavior whereby a male otter will use his teeth to grasp the female's nose from behind. The male then clasps the female's torso from behind and inserts the penis into the vulva (Kenyon 1969, Packard and Ribic 1982).

Sea otters exhibit several modes of locomotion. Swimming behavior is most easily recognized when the otter is floating belly-up on the surface of the water. The otter is propelled through the water by use of one or both rear flippers. Porpoising behavior consists of short, forward leaps through the water as a means for high-speed locomotion. Patrolling behavior is exhibited by territorial males. The male swims belly-down, and only the head and back are visible moving along the surface (Packard and Ribic 1982, Pearson and Davis 2005). The sea otter's short front legs and elongated, flat back flippers make locomotion on land very awkward, and it is therefore rarely seen (Kenyon 1969, Packard and Ribic 1982).

Resting is an activity that typically occurs on the surface of the water, although otters occasionally haul out on land. The otter floats belly-up and the rear flippers are raised out of the water (usually folded across the otter's abdomen). The otter's eyes may be open or closed, and the otter's head may turn in various directions. However, no other activity is performed during resting bouts (Packard and Ribic 1982). Resting is the only activity, other than interacting, in which otters tend to associate with others in groups called rafts (Riedman and Estes 1990).

Foraging behavior begins with a recognizable foraging dive. During a foraging dive, the sea otter's head, shoulders and torso rise out of the water as it inflates its lungs. The torso bends forward and the head, shoulders, torso and tail re-enter the water in succession (Packard and Ribic 1982). Foraging occurs

on the sea floor and, whenever present, within the kelp canopy and understory. Most foraging dives occur in the subtidal zone in water <25 m deep, although foraging in water up to 100 m deep also occurs (Estes 1980, Garshelis 1983, Riedman and Estes 1988, VanBlaricon 1988, Wolt et al. in prep). Sea otters capture prey with their forepaws, then bring the prey to the surface to be consumed. The capture of burrowing prey such as clams requires the excavation of sediments. Sea otters are capable of displacing large volumes of sediment, and excavations can be up to 1 m deep (Kvitek and Oliver 1988, Riedman and Estes 1988). A sea otter may capture two or more prey items of the same or different species in a single dive, often storing them within the loose flaps of skin beneath each foreleg (Kenyon 1969, Riedman and Estes 1988). In some instances, sea otters use rocks or other objects as tools to crack open the exoskeletons of prey (Garshelis 1983, Riedman and Estes 1990).

Diet

The diet of California sea otters consists almost exclusively of benthic macroinvertebrates, most commonly crustaceans, mollusks (bivalves, gastropods, and cephalopods), and echinoderms (Estes et al 1981, Riedman and Estes 1988,1990; Estes and Bodkin 2002). In contrast, Alaskan and Russian sea otter diets also include epibenthic fish (Estes et al 1981, Riedman and Estes 1988,1990). A complete list of the 150 species reported as sea otter prey is provided by Estes and Bodkin (2002). Diet is related to habitat type and time of year. In soft-sediment communities, sea otters feed primarily on bivalve

mollusks, while epibenthic prey such as crabs and sea urchins predominate the diet in rocky habitats (Estes 1980, Riedman and Estes 1988). Although the diet of the sea otter population in a given area may be fairly broad, individual otters tend to specialize in certain prey, usually restricted to 1-3 species (Riedman and Estes 1990, Estes et al. 2003). These individual dietary patterns are similar between mothers and pups, indicating maternal transmission (Estes et al. 2003).

Physiology

Marine mammals exhibit higher resting metabolic rates than do terrestrial mammals (Yeates et al. 2007). However, sea otters represent an extreme, exhibiting resting metabolic rates that range from 2.8 to 3.2 times the levels predicted for a terrestrial mammal of similar size (Iverson 1972, Morrison et al. 1974, Costa 1978, Costa and Kooyman 1984, Yeates et al. 2007). Sea otters also have a higher surface area from which to lose heat relative to the tissue volume within which to produce or retain heat, in comparison to larger marine mammals. Furthermore, other marine mammals depend on an internalized blubber layer for insulation; whereas, sea otters use their dense fur-covering to trap an air layer against their skin and thus prevent excess heat loss to the water (Williams et al. 1992). However, it is possible that the air layer compresses as the otter dives, thereby reducing the insulative value of the fur covering. Because of this, the otter tends to have elevated thermal energetic costs. These costs must be compensated for by activity, shivering, or by the heat produced by food processing (Costa and Kooyman 1984).

Social Structure

Sea otters are sexually segregated when not breeding, with adult males and females separated by distances up to 150 km (Garshelis et al. 1984, Riedman and Estes 1990). Reports indicate that approximately 97% of the otters in “male areas” are male, both juveniles and breeding-age adults (Garshelis 1983, Gilkinson 2004). A male area generally occurs at the edges of the range where expansion is taking place, and is usually found in an area with abundant food resources but is less protected from rough sea conditions (Estes 1980, Garshelis et al. 1984, Riedman and Estes 1990). “Female areas” are more likely to be found in areas with decreased prey availability, but are more protected and suitable for raising young (Garshelis et al. 1984, Riedman and Estes 1990). Males will enter these areas in order to establish and maintain breeding territories, thereby accounting for 11-31% of the population in female areas (Garshelis et al. 1984, Jameson 1989, Riedman and Estes 1990).

Females reach sexual maturity at approximately 4 years old (Kenyon 1969, Garshelis 1983, Jameson and Johnson 1993). Males reach sexual maturity at 5-6 years old, but may not be able to hold territories until 8-10 years old (Garshelis 1983, Rotterman and Simon-Jackson 1988). Territories are formed for the purpose of breeding, excluding other males and testing the sexual receptivity of females that enter the territory. Territorial males often patrol the boundaries of their territories, and leave only for brief feeding excursions (Calkins and Lent 1975, Garshelis et al. 1984, Riedman and Estes 1990).

Territory holders typically rest in the main entranceway of their territories, and deter trespassers either without actual contact, or brief aggressive interactions (Garshelis et al. 1984, Riedman and Estes 1990). Mating success can vary with territory quality, duration of territory occupation, age, and size of the male. Larger males tend to hold higher-quality territories than smaller, younger males (Garshelis et al. 1984).

Human Impact

The earliest record of commercial sea otter exploitation began in the 1740's with the discovery of Alaska and the Aleutian Islands (Riedman and Estes 1990), and the species was decimated to near extinction by the end of the 19th century (Kenyon 1969). It is estimated that only 1,000-2,000 sea otters in approximately 13 populations remained, from an estimated total population of 150,000-300,000, when the species received protection from the International Fur Seal Treaty in 1911 (Kenyon 1969, Riedman and Estes 1990). Sea otter populations grew at a rate of 15% per year during the early phases of recovery (Kenyon 1969), and the species received additional protection in the United States from the Marine Mammal Protection Act of 1977, but they have not fully reoccupied their historical range (Reeves et al. 2002).

Study Area

This study was conducted in Simpson Bay (ca. 60.6^{o} N Lat., 145.9^{o} W Long.), a shallow fjord located in northeastern Prince William Sound, Alaska. Male sea otters began to reoccupy eastern Prince William Sound in the late

1970s. Simpson Bay specifically was reoccupied in 1977 and served as a male area until 1983-1985 when it became a predominantly female area (Garshelis et al. 1984, Kenyon 1969, Monnett and Rotterman 1988). Due to its location, Simpson Bay was not affected by the 1989 Exxon Valdez oil spill, which killed an estimated 2,787 sea otters in other parts of the sound (Riedman and Estes 1990).

Simpson bay is composed of 3 bays (north, west, and east), with a total area of ca. 21km^2. Summer sea surface temperatures range from 12^o to 14^o C, and surface salinities are approximately 18-20 gm kg^{-1} (Gay and Vaughn 2001, VanBlaricom 1988). The average precipitation is 415 cm^{-yr}, and wind-speed averages range from 4-14 km^{-h} during the summer (Gay and Vaughn 2001). Clams are the principle prey item (Garshelis 1983, Riedman and Estes 1988, Estes and Bodkin 2002), and the benthic habitat of Simpson Bay is mainly soft sediment with occasional rocky outcrops, and no large-bodied kelp (Gilkinson 2004). The bay is well protected from ocean swells, and is currently used during the summer by 100-150 sea otters, including female sea otters and their dependent pups, single females and territorial males (Gilkenson 2004).

Study Objectives

The main purpose of this project was to improve the understanding of sea otter behavior and ecology. The sea otter populations in Prince William Sound have received relatively little attention in comparison to the populations in California and the Aleutian Islands.

Tattoos, dyes, brands, colored or numbered tags, and other artificial marks, have been the primary ways of identifying individual animals. These methods mandate that the animal be captured, which may injure the animal and researcher (McGregor and Peake 1998). Researchers are using natural color patterns, scars and other features more frequently to identify animals for which capture and marking are not desirable. This study assessed the performance of a new computer-assisted matching program, the Sea Otter Nose Matching Program (*SONMaP*), which uses blotch-pattern recognition algorithms to match the shape and location of scar tissue in relation to normal pigmentation of sea otter noses.

In the past, sea otter activity budgets have been monitored using radiotelemetry (Estes et al. 1986, Gelatt et al. 2002), or have been derived from time-depth recorders (Bodkin et al. 2007). This study aimed to evaluate the activity patterns of male sea otters in Simpson Bay, Prince William Sound, Alaska, using opportunistic individual follows and instantaneous sampling techniques. This method provides a non-invasive method of tracking and identifying individual sea otter behavior (Pearson et al. 2005). A 24-h scale energy budget was also created based on these activities and on previously documented energetics data (Yeates et al. 2007).

In addition, the size and quality of male territories within Simpson Bay were evaluated. Territory sizes were plotted using location points obtained during focal observations, and calculated using minimum convex polygons

(Odum and Kuenzler 1955) in ArcMap version 9.2 (Environmental Systems Research Institute, Inc. 2006). Territory quality was measured based on four distinct attributes: territory size, shoreline enclosure, accessibility, and prey availability. Ranks of each attribute were coded within a range of 0-2, and a summary quality score was calculated using Principle Components Analysis (PCA).

CHAPTER II

COMPUTER MATCHING OF SEA OTTER (*Enhydra lutris*) NOSE SCARS: A NEW METHOD FOR TRACKING INDIVIDUAL OTTERS*

Introduction

Recognition of individual animals enables detailed studies of movement patterns, foraging, life histories, survival, and is important for understanding the ecology and behavior of species (Würsig and Jefferson 1990, McGregor and Peake 1998). Artificial marks, such as tattoos, dyes, brands, colored or numbered tags, and telemetry (radio and satellite) have been the primary ways of identifying individual animals. However, these systems require that the animal be captured, which may stress or injure the animal and/or the researcher, and may modify the animal's behavior (McGregor and Peake 1998). Increasingly, researchers are using natural color patterns, scars and other features to identify animals in a wide range of taxa for which capture and marking is not desirable or logistically feasible (Langtimm et al. 1998). For example, sperm whales (Physeter macrocephalus) can be identified from marks on the trailing edges of the flukes (Arnbom 1987, Whitehead et al. 1997); boat propeller-inflicted scars can be used to identify sirenians (Langtimm et al. 1998);

* Reprinted with permission from "Computer matching of sea otter (*Enhydra lutris*) nose scars: a new method for tracking individual otters" by S.E. Finerty, G.R. Hillman and R.W. Davis, 2007. Aquatic Mammals, 33, 349-358. Copyright 2007 Aquatic Mammals.

and some pinnipeds can be identified by scars as well as unique pelage patterns (Forcada and Aguilar 2000, Forcada and Robinson 2006).

Foote (1970) first suggested that female sea otters could be identified by nose scars incurred during copulation. Several other studies have since used this method to a limited extent (Calkins and Lent 1975, Loughlin 1980, Garshelis 1983). Gilkinson (2004) was the first to use nose scars to identify individual Alaskan sea otters to study their movements and habitat associations. In that study, the size, shape and location of nose scars were used to distinguish individuals. Other characteristics such as pelage color around the head, length of vibrissae, tooth discoloration, and other marks or scars were also used. Image quality based on clarity, lighting and contrast, visibility of the nose, and distance to the animal affected the ability to match animals. Each image was then visually compared to every other image that had been previously recorded. In a catalog of 1,638 images, a single match required several hours of effort.

Computer-assisted matching programs have been developed for several cetacean species, including bottlenose dolphins (*Tursiops truncates*), humpback whales (*Megaptera novaeangliae*), and southern right whales (*Eubalaena australis*). Coded descriptions of identifying features such as the trailing edge of dorsal fins, fluke pigmentation patterns, or body patterns of callosities, were scored on digital images, then ranked against images in a catalog (IWC 1990). No computer-assisted matching program has been developed previously for use with sea otters. In this study, the performance of a new program (Sea Otter

Nose Matching Program (*SONMaP*) is described. *SONMaP* used blotch-pattern recognition algorithms to match the shape and location of lightly colored scar tissue in relation to normal black pigmentation of sea otter noses.

Methods

Digital Imaging of Sea Otters

This study was part of a long-term research program investigating the behavior and ecology of sea otters in Alaska (Gilkenson 2004). The study area was Simpson Bay (ca. 60.6^{o} N Lat., 145.9^{o} W Long.), located in northeastern Prince William Sound, Alaska (Figure 1). It is approximately 21 km^2 in area and is currently used during the summer by an average of 119 $\pm$ 9.3 SD sea otters, including adults and subadults (91 $\pm$ 6.8 SD) and pups (28 $\pm$ 3.8 SD) (Davis, unpub. obs.).

Digital images of sea otters were taken from June to August of 2002 and 2003, by Davis team researchers and volunteers, from a 6-m skiff using methods described by Gilkinson (2004). The research team was composed of a driver, photographer, recorder, spotter, and GPS operator. Images were taken with a Nikon D1H digital camera with an 80-400 mm image-stabilized telephoto lens. When an otter was sighted, the skiff driver approached the animal slowly while the photographer attempted to obtain a frontal image of the sea otter's face, usually at a distance of not less than 30 m. Contact was maintained with the animal until either the photographer expressed confidence in capturing a good image, or the otter actively avoided the boat.

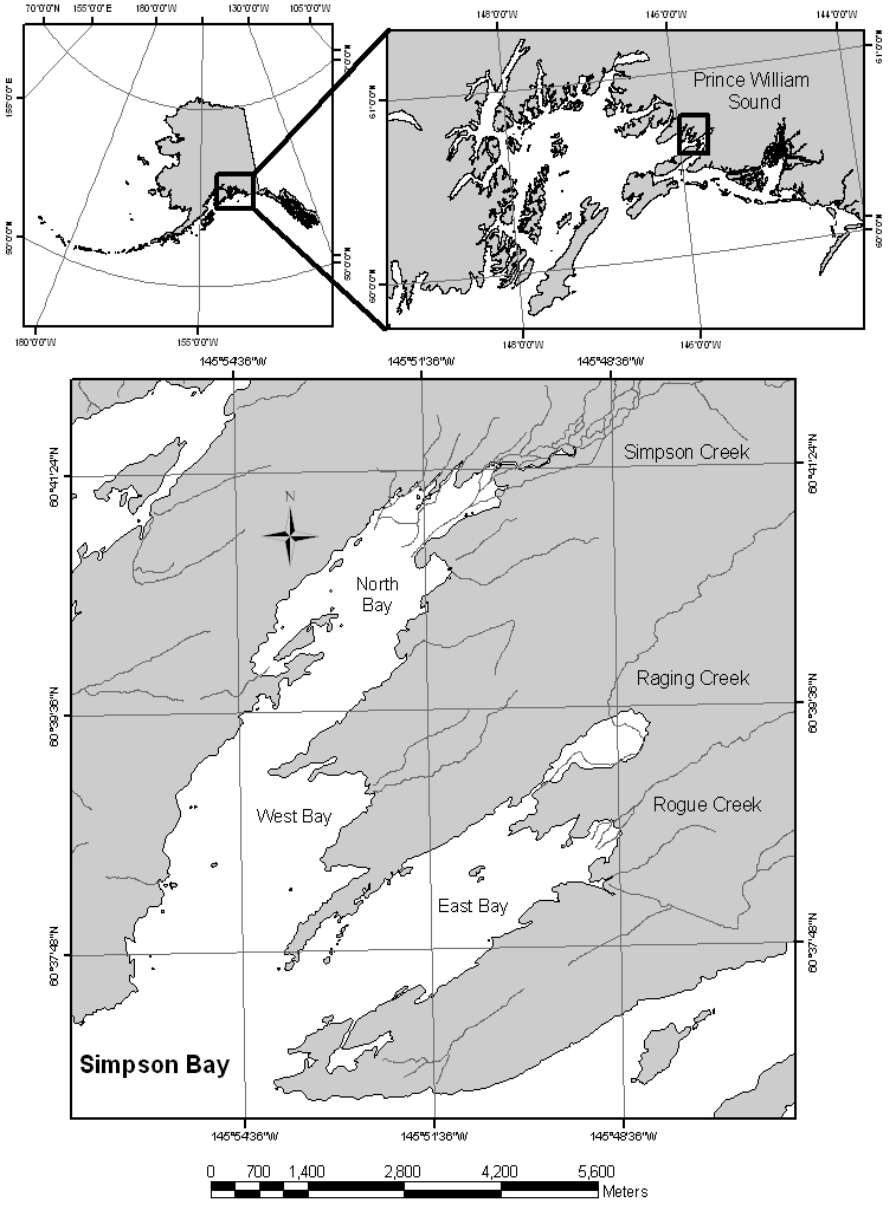


Figure 1. Simpson Bay, Prince William Sound, Alaska (Noll et al., 2009)

Image-Identification Analysis

The photo-identification method was believed to work for individual recognition because sea otters accumulate scars on their nose, apparent as a discoloration of pink or white, rather than the natural black skin color. These scars are acquired over a sea otter's lifetime from aggressive interactions between males, or during copulation when the male bites the female's nose to hold her in place for mating.

A catalog was created for the 806 images of sea otters taken in 2002, which was later combined with the images taken in 2003 to make a catalog of 1,638 images of otters (Gilkinson 2004). The images were evaluated for quality after each survey using *Adobe Photoshop* 7.0 (Adobe Systems, San Jose, CA). One to four of the best images (based on proximity, sharpness and head orientation) of each individual were cropped to isolate the face from the rest of the image. Then two researchers independently matched sea otters in these images by visually comparing them with all other images in the catalog. Only those matches identified by both individuals were used to assess the computer-assisted matching program. Ninety-six images (11.9%) were visually matched from the 2002 catalog, and 186 images (11.4%) were visually matched from the combined 2002-2003 catalog.

In this analysis, images of these previously matched otters (186 in total) were used to test the performance of *SONMaP*. The matching program, which used a blotch-pattern recognition algorithm based on the shape and location of

lightly colored nose scars, was developed by one of the authors (G. Hillman). The nose in each image was first isolated using *Adobe Photoshop* 7.0. Then, using *SONMaP*, the location of the pink or white scar tissue on the nose, in relation to the normal black tissue, was interactively marked with a computer cursor. A clustering algorithm then classified all points on the nose as scarred or not, based on similarity in intensity and color to the marked points. Three points at the center-top and extreme right and left sides of the nose were marked interactively to define the boundaries, and these points were used to guide an affine transformation which converted the nose image to a standard lozenge shape and then digitally normalized this shape to correct it for a frontal orientation. Each sea otter nose image was ranked based on quality (Q1 to Q4, Table 1, Figure 2) and distinctiveness (D1 to D5, Table 2, Figure 3) of the scars. Matching of any two images was accomplished by *SONMaP* by superimposing and subtracting the normalized nose images. The degree of similarity of two images was computed as the sum of the pixel-wise intensity values for all pixels that were present within the nose area of both images. When an image was used as a query, it was compared to all other images in the catalog, and the resulting differences were sorted by magnitude. The cataloged images were then presented to the user with the most similar first, and six images displayed at a time. The operator reviewed the proposed matches and confirmed or rejected the match, paging through the catalog if necessary until a match was

found. If no match was found, then the otter was entered into the catalog as a new individual.

Table 1: Rating system for normalized image quality

Rating[a]	Criteria
Q4	Excellent quality image. Background area is clear and dark (Good contrast). Edges of image are clean, not skewed. No possible glare or water spots visible.
Q3	Good quality image. May have one to two of the following minor flaws: edges of image are slightly skewed, image is slightly blurred, few small possible glare or water spots are visible.
Q2	Poor quality image. Displays all flaws listed in N3, or one to two of the following: one or two large possible glare or water spots visible, edges have major skews, image is pixilated, poor contrast.
Q1	Very poor quality image. Image very blurred and pixilated, or image displays more than 3 of the above flaws.

[a] Rating system is Q1-Q4, with Q4 indicating the highest quality images (Gilkenson, 2004)

Table 2: Rating system for normalized image distinctiveness

Rating[a]	Criteria
D5	Nose scars are highly distinctive including a large scar or scar pattern that is evident/distinctive even in a poor quality image.
D4	Nose has at least one distinctive medium-sized scar OR has two or more small or less distinctive scar/identifying features that form a distinctive pattern.
D3	Nose has one small scar/identifying feature of distinctive location or shape OR two or more very small scars forming a distinct pattern.
D2	Nose has some scars, but they are indistinct.
D1	No nose scars or other identifying features.

[a] Rating system is D1-D5, with D5 indicating the most distinctively marked individuals

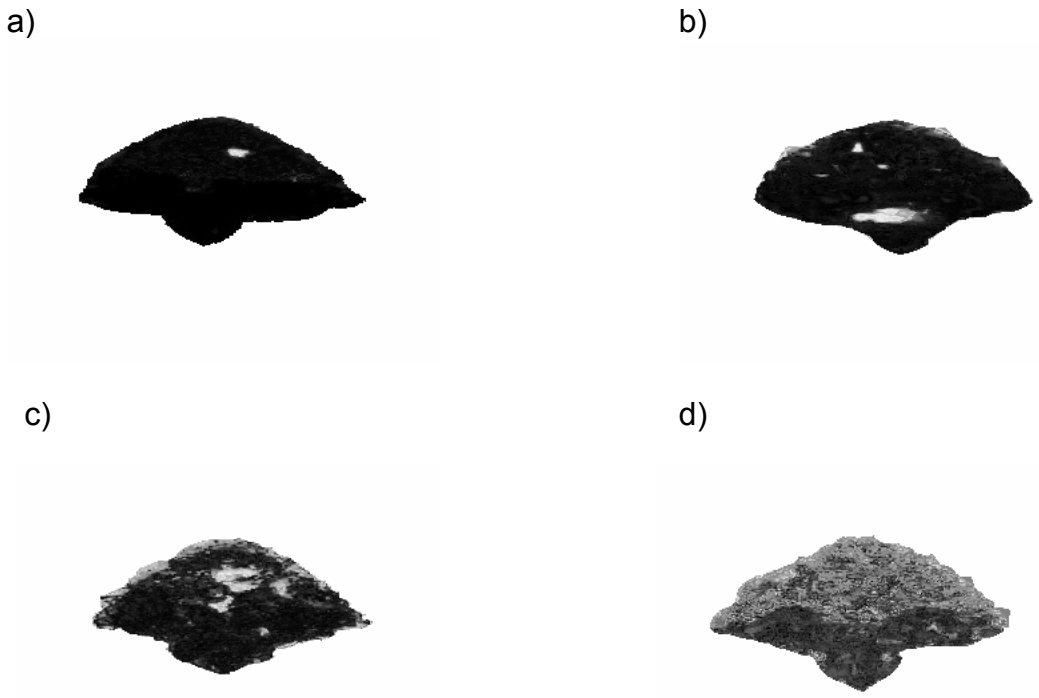


Figure 2. Normalized sea otter nose images listed from best to worst quality degrees. a) Q4, b) Q3, c) Q2, and d) Q1.

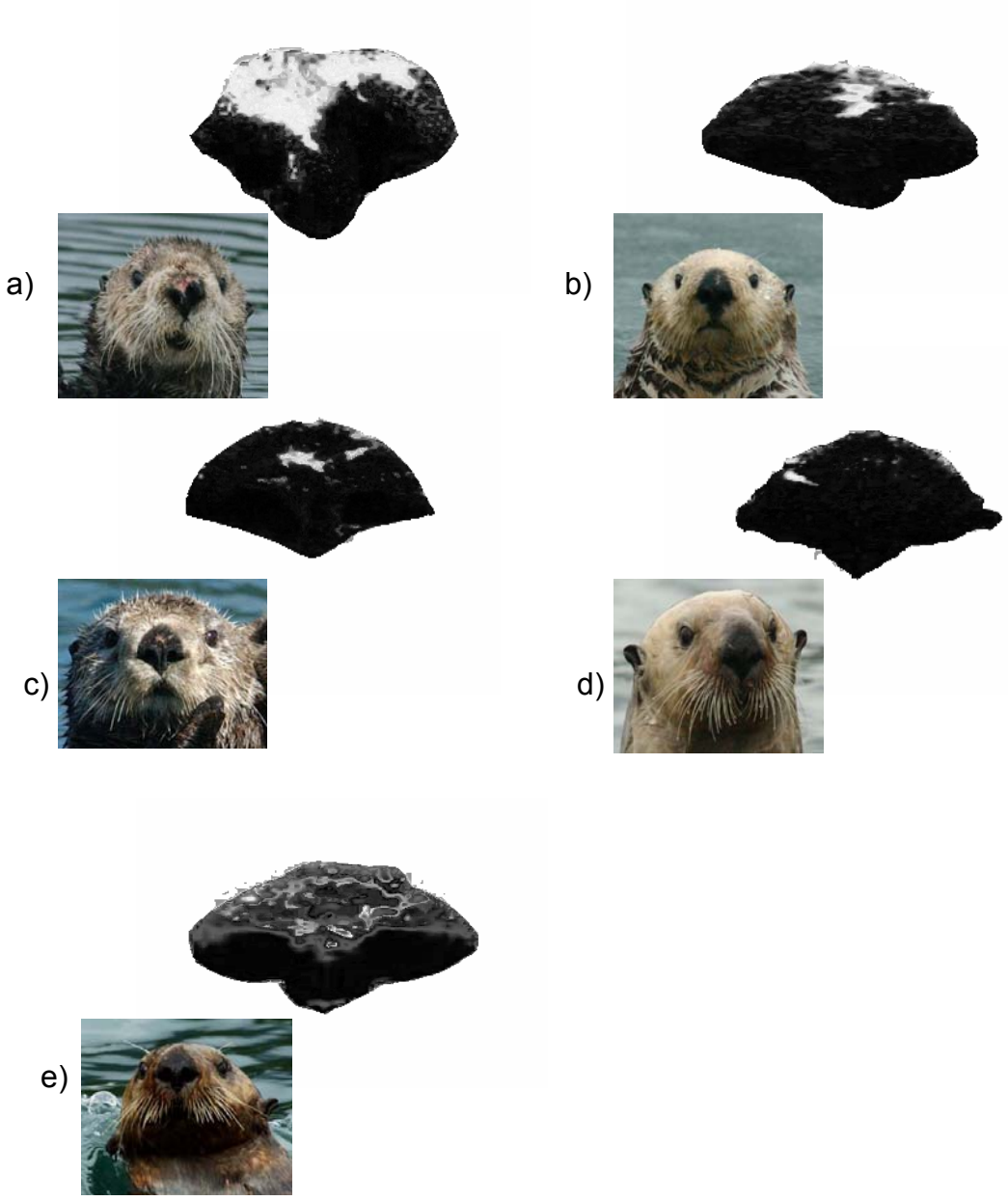


Figure 3. Normalized sea otter nose images listed from best to worst distinctiveness degrees. a) D5, b) D4, c) D3, d) D2, e) D1.

The images of sea otters that were matched by *SONMaP* were classified as BEST, AVERAGE or WORST if a correct match was found within the first 10%, 11-50%, or 51-100% of images in the catalog, respectively (Table 3). Since all of the sea otters used in this analysis had been visually identified previously, all images fell within one of the three classifications.

Contingency table analysis (Conover 1999) was used to determine if the distribution of images in each of the four quality and the five distinctiveness categories was uniform regardless of the BEST/AVERAGE/ WORST classification. Due to small sample sizes, exact p-values were calculated using a Monte Carlo simulation approach using *StatXact (Cytel* Software Corporation 1999). Standardized residuals plots (Lloyd 1999) were used to determine where the model did not fit these data. Significance was assessed at the 0.05 alpha level; tendencies were assessed at the 0.10 level of significance.

Results

Normalized image quality and normalized image distinctiveness values were tested separately for both catalogs (2002 catalog alone and the 2002-03 combined catalog; Tables 4-7). The first null hypothesis was that the distribution of images in the quality categories for each catalog was uniform regardless of BEST/AVERAGE/ WORST classification:

$$H_o: P(i,j) = 0.25 \text{ for } i=1\ldots4 \text{ and } j=1\ldots3$$

This null hypothesis was rejected (2002: $X^2 \geq 47.4$, $p=0.00005$; 2002-03: $X^2 \geq 21.7$, $p=0.00995$) for both catalogs. Based on the standardized residuals, there

Table 3: Image classification criteria

	Classification Percentage Limit	2002 Catalog (806 Images)	2002-2003 Catalog (1638 Images)
BEST Classification [a]	Matched within first 10% of catalog	Matched within images 1-81	Matched within images 1-164
AVERAGE Classification	Matched within first 50% of catalog	Matched within images 82-403	Matched within images 165-819
WORST Classification	Matched within first 100% of catalog	Matched within images 404-806	Matched within images 820-1638

[a] Classification of BEST/MID/WORST based on the match position in catalog

Table 4: Normalized image quality results for 2002 catalog (N= 96)

Data (Observed Matrix):

2002	Quality			
	N1	N2	N3	N4
Best	1	12	17	32
Average	0	9	9	7
Worst	5	1	3	0

Expected Matrix:

2002	Qualify			
	N1	N2	N3	N4
Best	15.5	15.5	15.5	15.5
Average	6.3	6.3	6.3	6.3
Worst	2.3	2.3	2.3	2.3

Standardized Residual Matrix:

2002	Quality			
	N1	N2	N3	N4
Best	**-3.68**	-0.89	0.38	**4.19**
Average	**-2.50**	1.10	1.10	0.30
Worst	*1.83*	-0.83	0.50	-1.50

Bold values indicate significant standardized residuals (α= 0.05). Italicized values signify standardized residuals that indicate tendencies (α = 0.10)

Table 5: Normalized image distinctiveness results for 2002 catalog (N= 96)

Data (Observed Matrix):

2002	Distinctiveness				
	D1	D2	D3	D4	D5
Best	3	8	15	19	17
Average	2	5	6	9	3
Worst	4	4	1	0	0

Expected Matrix:

2002	Distinctiveness				
	D1	D2	D3	D4	D5
Best	12.4	12.4	12.4	12.4	12.4
Average	5.0	5.0	5.0	5.0	5.0
Worst	1.8	1.8	1.8	1.8	1.8

Standardized Residual Matrix:

2002	Distinctiveness				
	D1	D2	D3	D4	D5
Best	**-2.67**	-1.25	0.74	*1.87*	1.31
Average	-1.34	0.00	0.45	*1.79*	-0.89
Worst	*1.64*	*1.64*	-0.60	-1.34	-1.34

Bold values indicate significant standardized residuals (α= 0.05). Italicized values signify standardized residuals that indicate tendencies (α = 0.10)

Table 6: Normalized image quality results for 2002-2003 catalog (N= 186)

Data (Observed Matrix):

2003	Quality			
	N1	N2	N3	N4
Best	9	26	35	21
Average	11	24	17	23
Worst	5	4	5	6

Expected Matrix:

2003	Quality			
	N1	N2	N3	N4
Best	22.8	22.8	22.8	22.8
Average	18.8	18.8	18.8	18.8
Worst	5.0	5.0	5.0	5.0

Standardized Residual Matrix:

2003	Quality			
	N1	N2	N3	N4
Best	**-2.88**	0.68	**2.57**	-0.37
Average	*-1.79*	1.21	-0.40	0.98
Worst	0.00	-0.45	0.00	0.45

Bold values indicate significant standardized residuals (α= 0.05). Italicized values signify standardized residuals that indicate tendencies (α = 0.10)

Table 7: Normalized image distinctiveness results for 2002-2003 catalog (N= 186)

Data (Observed Matrix):

2003	Distinctiveness				
	D1	D2	D3	D4	D5
Best	6	13	15	34	23
Average	12	22	11	17	8
Worst	5	4	2	3	6

Expected Matrix:

2003	Distinctiveness				
	D1	D2	D3	D4	D5
Best	18.2	18.2	18.2	18.2	18.2
Average	14.0	14.0	14.0	14.0	14.0
Worst	4.0	4.0	4.0	4.0	4.0

Standardized Residual Matrix:

2003	Distinctiveness				
	D1	D2	D3	D4	D5
Best	**-2.86**	-1.22	-0.75	**3.70**	1.13
Average	-0.53	**2.14**	-0.80	0.80	*-1.60*
Worst	0.50	0.00	-1.00	-0.50	1.00

Bold values indicate significant standardized residuals (α= 0.05). Italicized values signify standardized residuals that indicate tendencies (α = 0.10)

were significantly more Q4 images and fewer Q1 images in the 2002 BEST classification, and fewer Q1 images in the 2002 AVERAGE classification.

There was a tendency for more Q1 images to occur in the 2002 WORST classification (Table 4). In the 2002-03 combined catalog, there were significantly fewer Q1 images, and significantly more Q3 images in the BEST classification. The AVERAGE classification had a tendency for fewer Q1 images (Table 6).

The second null hypothesis was that the distribution of images in the distinctiveness categories for each catalog were uniform regardless of BEST/AVERAGE/ WORST classification:

$$H_o: P(i,j) = 0.20 \text{ for } i=1..5 \text{ and } j=1..3$$

Again, this null hypothesis was rejected (2002: $X^2 \geq 29.8$, p=0.00275; 2002-2003: $X^2 \geq 37.2$, p=0.00060) for both catalogs. The standardized residuals in the 2002 BEST classification had significantly fewer D1 images, and a tendency for more D4 images. The 2002 AVERAGE classification had a tendency for more D4 images, while the 2002 WORST classification had a tendency for more D1 and D2 images (Table 5). In the 2002-03 combined catalog, the BEST classification had significantly fewer D1 images and significantly more D4 images, and the AVERAGE classification had a tendency for more D2 images and a tendency for fewer D5 images (Table 7).

For the 2002 catalog, the true match was included in the BEST category for 69.6% of the previously visually matched images. For the 2002-2003 combined catalog, the true match was included in the BEST category for 48.9% of the previously visually matched images. Of the images in the BEST category, 28.2% of the correct matches were included in the first 9 images listed by *SONMaP* in the 2002 catalog and 16.1% for the combined 2002-2003 catalog.

On average for the 2002 catalog, a match was confirmed within the first 113 of 806 images (first 14%) selected by the software. For the combined 2002-2003 catalog, a match was confirmed, on average, within the first 328 of 1,638

images (first 20%) classified initially. By comparison, a match was found, on average, within the first 50% of each catalog (403 out of 806 images in the 2002 catalog; 819 out of 1,638 images in the 2002-03 catalog) without the use of *SONMaP.*

For each image, approximately 30 s were needed to visually compare one image with another to ascertain a match. When *SONMaP* was used, an average of 56.5 min (0.9 h) were needed to confirm a match in the 2002 catalog, and an average of 164 min (2.7 h) were needed to confirm a match in the 2002-2003 catalog. Without *SONMaP*, an average of 201.5 min (3.4 h) were needed to confirm a match in the 2002 catalog, and an average of 409.5 min (6.8 h) were needed to confirm a match in the 2002-2003 catalog. On average, it took 3 times longer to find a match without *SONMaP*.

Discussion

Several computer assisted identification programs have been developed to identify individual marine mammals from a catalog of images (Whitehead 1990, Huele et al. 2000, Hillman et al. 2003, Beekmans et al. 2005). As with *SONMaP*, each of these systems uses coded descriptions of different anatomical features that are digitally scored, then ranked against images already in the catalog. Currently, there are three computer assisted photo-identification methods available for cetaceans. *Highlight* (Whitehead 1990, Beekmans et al. 2005) and *Europhlukes* (Huele et al. 2000, Beekmans et al. 2005) are used to identify sperm whales, while *Finscan* (Hillman et al. 2003) is a program that was

developed for identifying delphinids. Individual sperm whales were identified by comparing the markings on the trailing edge of the flukes (IWC 1990), and individual delphinids are identified by the pattern of nicks and notches found along the trailing edge of the dorsal fin (IWC 1990, Hillman et al. 2003).

The computer-matching process for each program is similar, although the matching algorithms differ. As with *SONMaP*, each image is compared with those already cataloged. Each method uses a matching algorithm that computes a match coefficient for each comparison (Whitehead 1990, Hillman et al. 2003, Beekmans et al. 2005). Each program then produces an ordinal list of the best possible matches. The user visually checks the proposed matches and makes a final decision (Hillman et al. 2003, Beekmans et al 2005).

The *Highlight* and *Europhlukes* programs were both tested using a test set consisting of 592 photographs representing 296 matched pairs of different sperm whales (Beekmans et al. 2005). As with *SONMaP*, a rating system was developed for these images. Each image was assigned a numerical rating of 1-5 based on the quality of the image. Each image was also assigned to one of three distinctiveness classes. The distinctiveness of each trailing edge was represented by the number of marks on the fluke. Class 1 included flukes with less than 10 marks, Class 2 included flukes with 10 to 20 marks, and Class 3 included flukes with over 20 marks (Beekmans et al. 2005).

For both methods, the quality of the images and distinctiveness of the marks contributed to the accuracy of the matching program. Of the true

matches, 87.6% were included in the top nine images of the ordinal list produced by *Highlight*, and 86.0% of the true matches were included in the top nine matches of the ordinal list produced by *Europhlukes* (Beekmans et al. 2005).

Images of animals with greater fluke distinctiveness (more features) were matched more accurately by each method. There were 124 images assigned to Class 1 (least distinctive). Of these images, 51.6% of the true matches were included in the top nine images presented by the ordinal list using *Highlight*, and 57.3% of the images were not included using *Europhlukes*. Of the 354 Class 2 (moderately distinctive) images, 82.5% of the true matches were listed in the top nine images presented by *Highlight*, and 78.5% were included using *Europhlukes*. Of the 114 Class 3 (most distinctive) images, 93.0% of the true matches were included in the top nine using *Highlight*, and 94.7% of the true matches were included using *Europhlukes* (Beekmans et al. 2005). With the *SONMaP* system, the true match was included in the BEST category for 69.6% of the 2002 catalog, and for 48.9% of the 2002-2003 combined catalog. Of these images, 28.2% of the matches were included in the top 9 for the 2002 catalog, and 16.1% were included in the top 9 for the 2002-2003 combined catalog.

Images of dusky dolphin (*Lagenorhynchus obscurus*) dorsal fins were used to test the performance of the *Finscan* system. Each processed dorsal fin image was compared by *Finscan* to each of the 65 other images in one test set. Also, to test the efficiency of the system when using a larger catalog, each

image was tested a second time against a catalog of 250 images, and a third time against a catalog of 650 images (Markowitz et al. 2003). The average number of digital images presented by this system before the true match was 4 out of 65, 15 out of 250, and 45 out of 650 images, meaning that the true match occurred within ca. the first 6% of each catalog (Markowitz et al. 2003). The average number of images presented by the *SONMaP* system before the true match was 113 out of 806, or 14% of the 2002 catalog, and 328 out of 1,638, or 20% of the 2002-03 combined catalog. Overall, *SONMaP* did not perform as well as *Highlight*, *Europhlukes* or *Finscan* for identifying the true match in the top 9 images. This may reflect either inherent differences in the performance of the matching algorithms, or the requirement for images of high quality and distinctiveness to appear in the top 9 images for *SONMaP*.

Results indicate that *SONMaP* can be used to help identify individual sea otters with nose scars from a large catalog. Nose scars in adult females result from injuries received during copulation, when the male grasps the female by the nose and upper lip with its teeth (Foott 1970, Estes and Bodkin 2002, Gilkinson 2004). There is little published information on the nose scars in adult males. The source of these scars is most likely the result of antagonistic interactions with other males (Davis, unpublished observations).

A high degree of stability of natural marks is desirable if they are to be used for identification (Pennycuick 1978). Neither this study, nor the study by Gilkinson, (2004) investigated the stability of sea otter nose scars over time,

therefore, it is unknown. Eight individuals were identified via their natural marks in both years, thus some scars were stable for a least one year (Gilkinson 2004). Since female otters will mate every year (Riedman and Estes 1990, Jameson and Johnson 1993), there is the possibility that scars will change annually. Nevertheless, several females with pups were observed without nose scars during the course of this study, which indicates that not all copulations result in scarring.

As with the aforementioned programs, the accuracy of *SONMaP* appears to be highly dependent on the quality of the image and the distinctiveness of the marks. The *SONMaP* system was tested using previously matched images as opposed to only images of higher quality. The image catalogs used in this study were also larger (2002 catalog = 806 total images, 2002-2003 catalog= 1,638 total images) than the catalogs of other matching programs. These factors must be considered when comparing the abilities of the *SONMaP* system to other computer-assisted matching programs.

The limitations of *SONMaP* are similar to other matching programs. Unequal capture probability is a potential problem in sea otter photo-identification, as well as in other studies (Pennycuick 1978, Whitehead 2001, Gilkinson 2004). Certain sea otters are more easily approached by the photographer than others (Finerty, unpublished observations), which produces better quality images for those individuals (IWC 1990). The matching of images is not only influenced by image quality, but also by the method used, the

distinctiveness of the marks, and the user (Carlson et al. 1990, Beekmans et al. 2005). The most likely sources of error to the system are loss or changes of the original marks, which can lead to a known individual to be identified as a new individual. Major changes in marks can also lead to false positives in which multiple individuals are identified as the same individual (Langtimm et al. 1998). However, the *SONMaP* catalog is constantly updated with the most recent images of each individual. Therefore, subtle changes in nose scars can be tracked over time, allowing the operator to correctly identify known individuals.

SONMaP is a user dependent program. As in other programs, the user must assign descriptions of marks, and thereby decide how the marks should be interpreted. If the images are to be processed over a number of years, it is likely that input for the matching program will be generated by different users. The more decisions that are made by the user, the higher the probability of inconsistency and error (Beekmans et al. 2005). A user training program would increase consistency in the use of *SONMaP* and other matching programs.

CHAPTER III

SUMMER ACTIVITY PATTERN AND FIELD METABOLIC RATE OF ADULT MALE SEA OTTERS (*Enhydra lutris*) IN A SOFT-SEDIMENT HABITAT IN ALASKA*

Introduction

One of the earliest descriptions of male sea otter behavior in Alaska was by Kenyon (1969). He described territoriality as being weakly expressed in sea otters, but later studies showed territoriality to be a prominent behavior in adult males. Studies of territorial male sea otter behavior have since been conducted in California (Vandevere 1970, Loughlin 1980, Jameson 1989, Ralls and Siniff 1990), and Alaska (Calkins and Lent 1975, Garshelis et al. 1986, Gelatt et al. 2002, Pearson and Davis 2005, Bodkin et al. 2007). Sea otters are sexually segregated when not breeding (Garshelis et al. 1984, Riedman and Estes 1990). In expanding populations, male sea otters are the first to explore new, prey-rich areas (Garshelis et al. 1984). Prior to the protection of sea otters under the International Fur Seal Treaty in 1911, the sea otter population in Prince William Sound (PWS), Alaska, had been reduced by commercial hunting. Currently, the PWS population of sea otters is listed as stable or increasing under the Endangered Species Act (Fish and Wildlife Service 2005). Male sea

* Reprinted from Journal of Experimental Marine Biology and Ecology, 377, S.E. Finerty, R.C. Wolt and R.W. Davis, Summer activity pattern and field metabolic rate of adult male sea otters (Enhydra lutris) in a soft sediment habitat in Alaska, 36-42, Copyright (2009), with permission from Elsevier.

otters began to re-inhabit eastern PWS in the late 1970s. Simpson Bay remained a male area until the 1980s (Garshelis et al. 1984, 1986), but is now used by territorial males and females with pups (Gilkenson 2004, Pearson et al. 2006).

In Alaska, adult males establish territories during the summer and autumn (Pearson and Davis 2005). Males enter areas preferred by females and establish resource-based breeding territories during non-winter months (Garshelis et al. 1984, Jameson 1989, Pearson et al. 2006). The peak of breeding occurs during the autumn in PWS, although evidence of copulations has been reported for all seasons (Garshelis et al. 1984).

Maintaining a territory can be energetically expensive for males (Kodric-Brown and Brown 1978, Pearson et. al. 2006) and may have negative consequences including 1) decreased time available for foraging and resting 2) increased energy expenditure due to courtship, mating and defense activities (e.g., patrolling boundaries) and 3) risk of injury or death due to agonistic encounters with conspecifics and predation (Clutton-Brock et al. 1988, Apollonio et al. 1989, Vehrencamp et al. 1989, Gosling and Petrie 1990, Isvaran and Jhala 2000, Pearson et al. 2006). However, territoriality increases access to females and therefore enhances reproductive success (Vehrencamp et al. 1989, Rosser 1992, Isvaran and Jhala 2000, Bro-Jorgensen and Durant 2003, Pearson et al. 2006).

Marine mammals exhibit higher resting metabolic rates than terrestrial mammals (Yeates et al. 2007). However, sea otters represent an extreme, exhibiting resting metabolic rates that are ca. 3 times the allometric prediction for a terrestrial mammal of similar size (Davis et al. 1988, Iverson 1972, Morrison et al. 1974, Costa 1978, Costa and Kooyman 1984, Yeates et al. 2007). Since sea otters are the smallest marine mammal, they also have the highest surface-to-volume ratio, which increases potential heat loss. In addition, other marine mammals depend on a subcutaneous blubber layer for insulation, whereas sea otters rely on fur to trap an air layer next their skin for thermal insulation (Williams et al. 1992). This air layer compresses as the otter dives, thereby reducing insulation. As a result, sea otters experience elevated thermal energetic costs which are offset by an increased resting metabolic rate, increased activity, and by the heat produced during food digestion and assimilation (HIF, Heat Increment of Feeding, Costa and Kooyman 1984).

In previous studies, sea otter activity budgets have been made using scan sampling (Estes et al. 1986), radiotelemetry (Garshelis et al. 1986, Gelatt et al. 2002), or have been derived from time-depth recorders (Bodkin et al. 2007). The goal of this study was to assess the diel activity patterns of male sea otters in Simpson Bay, a fjord in northeastern Prince William Sound, Alaska, using individual-follows (Mann 1999) combined with instantaneous sampling (Altmann 1974, Lehner 1996, Mann 1999, Pearson et al. 2005). These sampling techniques were conducted during six hourly periods corresponding to dawn,

day, dusk, and night. The activity budgets were then used to estimate FMR based on previously measured energetic costs for different activities (Yeates et al. 2007).

Methods

Study Site

Simpson Bay (ca. 60.6°N Lat., 145.9°W Long.), located in northeastern Prince William Sound, Alaska (Figure 1), was used as the study site because of its reasonable size, protection from rough seas, and reliable presence of sea otters. It is composed of two arms (northwestern and southeastern) and is approximately 21 km^2 in area; 7.5 km long in the northwestern arm, 5 km long in the southeastern arm, and 2.5 km across at the widest point. The average depth is about 30 m, and the maximum water depth is 125 m. The bottom type is mostly glacial clay, silt, and gravel with some rocky hard reefs. There are no large-bodied kelps (e.g., *Nereocystis*) that form canopies, but large fronds of sugar kelp (*Laminaria saccharina*) cover the benthos in many areas of the bay from the subtidal to a depth of ca. 10 m (Davis, unpublished observations).

The bay was re-colonized by male sea otters in 1977, and females moved into the area between 1983-85 (Garshelis 1983, Rotterman and Simon-Jackson 1988, VanBlaricom 1988). For the past eight years, Simpson Bay has been occupied during the summer by an average of 118 $\pm$ 9.9 SD sea otters, including adults and subadults (90 $\pm$ 6.9 SD) and pups (29 $\pm$ 4.4 SD) (Davis, unpublished

observations). During the winter, the number of otters in the bay decreases to ca. 50, although where they disseminate is poorly understood. This research was conducted under a Letter of Confirmation No. MA-043219 from the U.S. Fish and Wildlife Service.

Focal Observations

Field observations of male sea otter behavior were conducted during the summers (early May through late August) of 2005 and 2006 using individual-follows (Mann 1999) and instantaneous sampling (Altmann 1974, Lehner 1996, Mann 1999, Pearson et al. 2005). The research team, composed of a driver, recorder and observer, conducted surveys from a 6 m skiff. A regular schedule was followed by dividing the bay into three sections: north bay, west bay and east bay. Each day, one of these sections was selected in rotation for making observations, and another section was selected as an alternate should logistical problems occur. Boat-based observers determined if an otter was male by the presence of a penile ridge or testicular bulge (visible through binoculars), or by observing copulatory or patrolling behavior. Patrolling is a form of locomotion whereby a male swims belly-down with its head out of the water while scanning the surface, presumably for receptive females or other territorial males. Female sea otters primarily float on their backs or swim submerged, making patrolling a conspicuous male behavior (Pearson et al. 2006).

Individual follows occurred approximately twice a day during one of four 6-hourly time periods corresponding with astronomical dawn (05:00-11:00), day

(11:00-17:00), dusk (17:00-23:00) and night (23:00-05:00). Individual follows lasted 31 minutes (minute 0-minute 30) and instantaneous samples (Altman 1974, Lehner 1996) were taken once per minute during which the behavioral state (foraging, grooming, interacting with another otter, resting, swimming at the surface, or patrolling) was recorded from a distance of ca. 30 m or greater so as to minimize the risk of altering the animals' behavior. Behaviors were identified based on descriptions by Packard and Ribic (1982). Latitude and longitude were also recorded every minute using a Global Positioning System (GPS).

Data Analysis

Time/activity budgets were created for each behavior observed during each of the four time periods, and over a combined of 24-h period. Multivariate analysis of variance (MANOVA) was used to test differences in the relative amount of time a male otter spent performing each of the six behaviors (dependent variables) among the four time periods (independent variables). MANOVA tests were performed using *SPSS, Version 15* statistical software (SPSS, Chicago, IL). The alpha level for these tests was set at 0.05. In addition, a canonical variants analysis (similar to a discriminate functions analysis) was run to determine those behaviors (independent variables) that characterized (i.e., best distinguished among) the variance in time spent among the four time periods (dependent variables). The canonical variants analysis was run using *CANOCO, Version 4.5* software (CANOCO, Ithaca, NY).

Field Metabolic Rate (FMR) was estimated by combining the oxygen consumption (ml O_2 min^{-1} kg^{-1}) for resting (13.3), feeding (21.6), grooming (29.4), swimming (29.6), and interacting (24.5) for captive otters (Yeates et al. 2007) with the activity budgets for the male otters in this study. Yeates et al. (2007) trained test animals to make voluntary dives and surface under a clear acrylic dome. Oxygen consumption was determined under four conditions: 1) resting on the surface, 2) grooming, 3) following serial foraging dives, and 4) following single non-foraging dives. Foraging costs were determined by measuring oxygen consumption following prey-searching dives. Test animals were trained to dive to the bottom of a 9.1 m deep, 4 m diameter seawater storage tower with the metabolic dome at the surface of the water. A rocky substrate along with 3-5 kg of live crabs (*Cancer* spp) and live mussels (*Mytilus edulis*) were placed at the bottom of the tank to simulate foraging conditions in the wild. The test otter was allowed to forage by making repeated dives to the bottom to collect prey items. Following the collection of the prey, the otter surfaced beneath the metabolic dome while handling and consuming prey. All measurements followed the methods of Williams et al. (2004b) using an open-flow respirometry system for aquatic mammals (Yeates et al. 2007). Behaviors in this study that did not fall into one of the classifications of Yeates et al. (2007) were categorized as 'other' (e.g., interacting with conspecifics). For purposes of comparison, this study considered 'patrolling' to be energetically similar to 'swimming' (following a description of swimming costs and behaviors for sea otters in Williams 1989),

and therefore the two categories were combined. The weight-specific FMR (kJ day^{-1} kg^{-1}) was calculated as the product of the energetic cost of each activity, a conversion factor of 2.0083 x 10^{-2} kJ ml^{-1} O_2 (Schmidt-Nielsen 1997), and the number of minutes per day spent in each activity (i.e., proportion of day in each activity times 1,440 min day^{-1}). The total FMR (MJ day^{-1}) was calculated as the product of the weight specific FMR and the mean body mass (27.7 kg) of adult male sea otters (Yeates et. al. 2007) divided by 1,000 to convert kJ to MJ. Adult, male Alaskan sea otters can range in body mass from 18-45 kg. The average weight of an adult male from Amchitka Island, Alaska is 28.3 kg (Riedman and Estes 1990). The 27.7 kg body mass reported by Yeates et al. (2007) for California otters was used in this study because of its similarity to the average body mass previously reported for adult male Alaska sea otters.

MANOVA was used to test differences in the proportion of estimated energy male otters spent performing each of the six behaviors (dependent variables) among the four time periods (independent variables). A canonical variants analysis, as well as a Monte Carlo simulation, was used to determine those behavioral categories (independent variables) that characterized the variance in energy spent among the four time periods (dependent variables). The independent variables having absolute t-values > 2.1 (comparable to an alpha of 0.05) were considered to be significant. The independent variables having t-values < 2.1, while not strictly significant, were assessed as tendencies, and showed very strong contributions to the final explanatory model.

Results

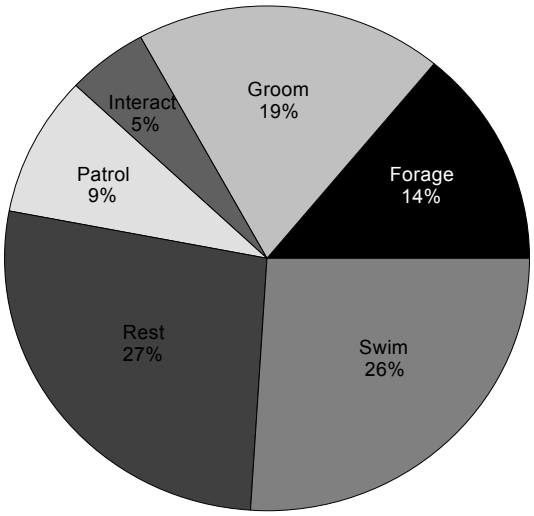
Research Effort

One hundred ninety focal observations (31 min each) were conducted for a total of 98 h; 25% (n = 47) occurred during the dawn (05:00-11:00 h local time), 28% (n = 53) occurred during the day (11:00-17:00 h local time), 26% (n = 49) occurred during the dusk (17:00-23:00 h local time) and 21% (n = 41) occurred during the night (23:00-05:00 h local time).

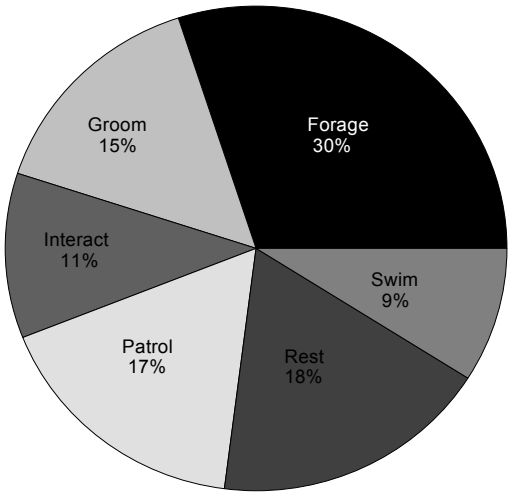
Activity Budget

A combined (all four time periods) 24-h activity budget was created for male sea otters based on the 190 focal observations (Figure 4a and Table 8). Approximately one-half of their time was spent in a combination of resting (27%) and swimming (26%), while grooming (19%) and foraging (14%) together accounted for one-third of the activity budget. Patrolling (9%) and interacting (5%) and accounted for the smallest portions of the activity budget.

The MANOVA showed that the four time periods did not explain a significant difference in mean time spent among the six behaviors. The Canonical Variants Analysis showed that the behavioral categories distinguished only 4.7% of the variance in time spent among the four periods, but a Monte Carlo simulation showed this to be statistically significant (F-ratio = 9.054; p=0.004). Interacting (t= 3.86) and Resting (t=2.71) were positively associated with dawn. Grooming (t=1.96), while not significant, also tended to be positively associated with dawn (Figure 5).



a)



b)

Figure 4. a) Twenty four hour activity budget for adult male sea otters in Simpson Bay, Alaska during summers (May to August) of 2005-06. b) Daytime only activity budget for adult male sea otters in Simpson Bay, Alaska during summer 2003 (Pearson et al. 2005)

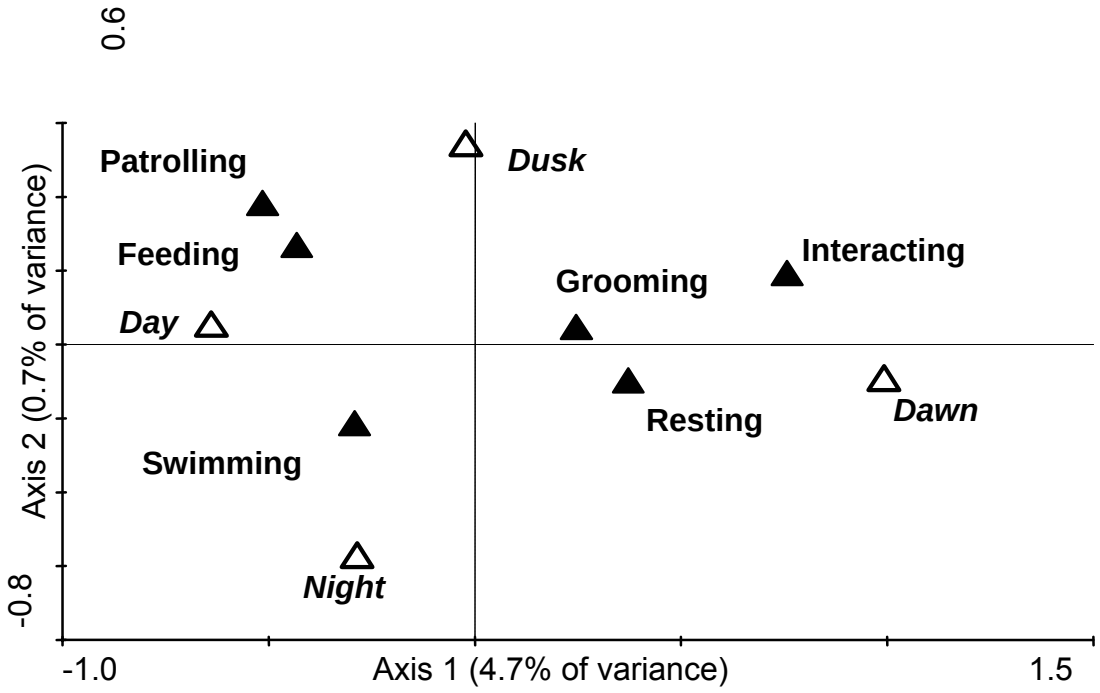


Figure 5. Results of the Canonical Variants Analysis showing associations on the first two canonical axes for behavioral categories and time spent among the time periods

Table 8. Daily activity budget and estimated Field Metabolic Rate (FMR) for adult male sea otters. Numbers in parentheses are the percentages of the total FMR

Behavior	Proportion of Day	Min per Day	FMR (kJ day^{-1} kg^{-1})	FMR (MJ day^{-1})
Resting	0.27	390	104.17	2.89 (15.2)
Feeding	0.14	207	89.80	2.49 (13.1)
Grooming	0.19	270	159.42	4.42 (23.2)
Swimming[a]	0.35	502	298.42	8.27 (43.4)
Other	0.05	71	34.93	0.97 (5.1)
Total	1.0	1,440	686.74	19.04 (100)

[a] Swimming includes the combined activities of swimming and patrolling

Estimated Field Metabolic Rate (FMR)

Based on this study's activity budgets and the energetic costs for different activities of sea otters in captivity (Yeates et. al. 2007), the weight-specific and total FMRs for each behavior were estimated (Table 8). The combined activity of swimming and patrolling (called swimming) accounted for the greatest percentage (43.4%) of energy expended each day. This was followed by grooming (23.2%), resting (15.2%), feeding (13.1%) and other (5.1%). The weight specific FMR for all activities was 686.7 kJ day^{-1} kg^{-1} and the total FMR was 19.04 MJ day^{-1}. This represents an FMR that was 6.6 times the estimated resting metabolic rate of 2.89 MJ day^{-1} (Table 8) and 2.2 times greater than the allometric prediction (FMR = 4.82 $Mb^{0.734}$) , where Mb is body mass in grams and FMR is kJ day^{-1}) for mammals generally (eutherian and metatherian) based on the doubly-labeled water method (Nagy 2005).

The MANOVA showed an overall significant difference ($p = 0.006$) in the relative amount of energy spent in each of the six behaviors among the four time periods. More energy was spent swimming during the day (estimated marginal mean = 0.008) than during the dawn (estimated marginal mean = 0.004). The Canonical Variates Analysis (Figure 6) showed that differences in relative amount of energy spent in the four time periods was not explained by the five behavioral categories (F-ratio = 3.432, $p = 0.272$). However, energy expenditure for feeding and swimming showed a more positive association with day, whereas, energy expenditure for grooming and resting showed a more positive association with dawn. The location of other behaviors near the center of the plot for the two strongest canonical axes (Figure 6), indicated that intermediate amounts of energy were spent in those behaviors among all time periods.

Discussion

Previous Studies of Male Sea Otter Activity Patterns

Studies of sea otter activity patterns have been conducted in Alaska and California using different methods, and considerable variability has been reported for time budgets (Table 9). Sea otters have large energy requirements due to an elevated metabolic rate (Costa and Kooyman 1982), and Kenyon (1969) estimated that they consume up to 25% of their body mass in food each day. Because of this, many of these previous studies focused on foraging behavior.

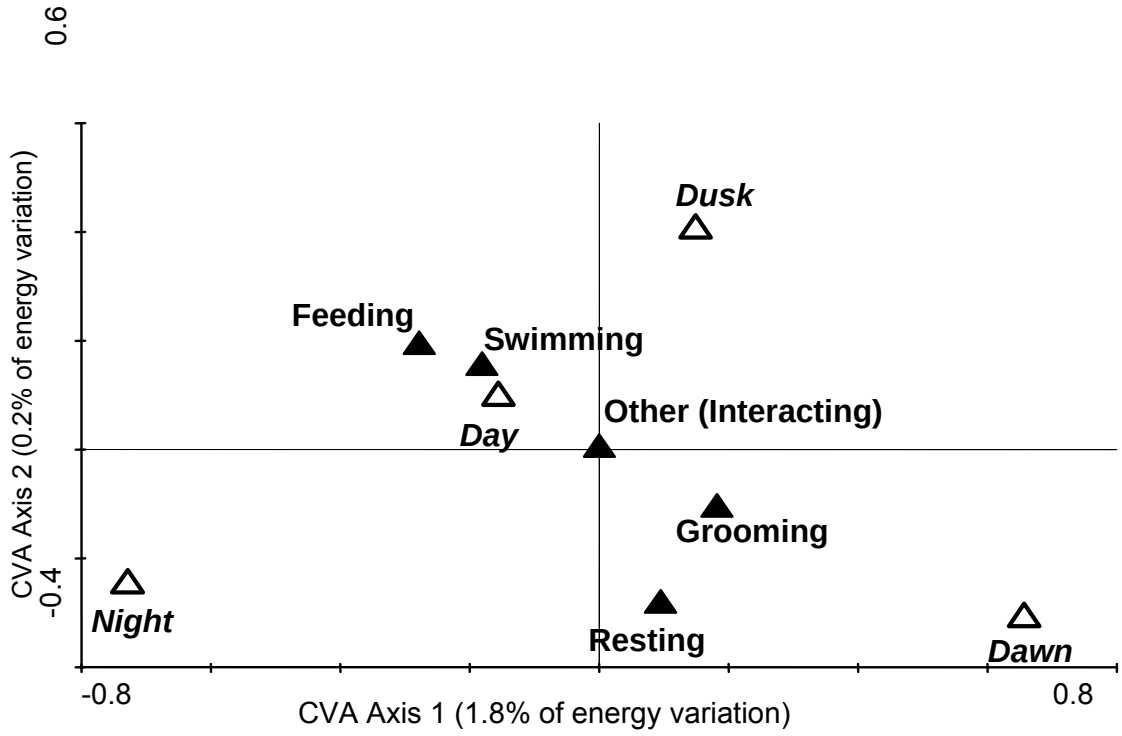


Figure 6. Results of the Canonical Variants Analysis showing associations on the first two canonical axes for behavioral categories and energy spent among the time periods. Note that in this analysis, patrolling and swimming have been combined into a single energetics category called swimming

Table 9. Comparison of sea otter activity budgets in Alaska and California

	% time spent [a]		
Study location (source)	Foraging	Resting	Swimming
Prince William Sound, Alaska (this study)[b,d]	14	27	26
Olympic Peninsula, Washington (Walker et al., 2008) [c,e]	8	62	8
Cross Sound, Alaska (Bodkin et al., 2007)[b,d]	28	54	N/A
San Simeon, California (Yeates et al., 2007)[c,d]	36	40	8.5
Prince William Sound, Alaska (Pearson et al., 2005)[c,d]	30	18	9
Amchitka, Alaska (Gelatt et al., 2002)[b,e]	38	45	N/A
Monterey to Piedras Blancas, California (Estes et al., 1986)[c,e]	24	59	N/A
Prince William Sound, Alaska (Garshelis et al., 1986)[b,e]	47	50	3

[a] Row totals do not all equal 100% due to different categories of activity presented by each study

[b] Behavior throughout the 24-h cycle

[c] Daytime behavior

[d] Adult male sea otters

[e] Adult sea otters, male and female

Radio Telemetry

Garshelis et al. (1986) and Gelatt et al. (2002) used radio telemetry to determine the activity budget of sea otters. Garshelis et al. (1986) conducted their study in the region around Green Island, in southcentral Prince William Sound, Alaska, where very high frequency (VHF) radio transmitters were attached to the rear flippers of 65 adult male otters. Radio signals were not detectable when the external whip antenna was submerged. This enabled activities to be categorized as foraging, resting or swimming on a 24-h basis. Signals from resting otters were uninterrupted because it was assumed that otters rest with their rear flippers exposed. Swimming was characterized by frequent, short interruptions as the radio-tags dipped below the water surface. Feeding dives and subsequent food consumption at the surface were characterized by long breaks in the signal, followed by periods that were uninterrupted. Based on these assumptions, this study concluded that males allocated 47% of their time to foraging, 50% to resting and 3% to swimming.

Gelatt et al. (2002) conducted their study around Amchitka Island, Alaska, where VHF radio transmitters were surgically implanted in 21 adult male otters that were monitored every 10 min for 24-h twice per week. Activities were categorized as foraging, resting and other. Using similar assumptions about signal pattens, the time budget from this study was similar to that of Garshelis et al. (1986) with adult male sea otters allocating 38% of their time to foraging, 45% to resting and 17% to other activities.

Time-Depth Recorders (TDR)

Bodkin et al. (2007) conducted their study near Cross Sound, located in southeastern Alaska. VHF radio transmitters and archival time-depth recorders were surgically implanted into 21 adult sea otters (5 males). Each TDR was programmed to record depth, with 0.25 m accuracy, at 2 second intervals for 46 days. Color-coded tags were attached to the hind flippers of each individual to allow for visual recognition. Instrumented animals were observed daily from both shore and boats. Activities were categorized as foraging, resting, and other (swimming, grooming, interacting). The males allocated 28% of their time to foraging, 54% to resting, and 18% to other diving behaviors (swimming, grooming, interacting).

Scan-sampling

Estes et al. (1986) used the scan-sampling method to determine the activity budget of sea otters in a rocky reef and kelp forest habitat in central California. Behavior was categorized as foraging, resting or other by observing a group of otters in an area at 30 min intervals with 10x binoculars. Due to low luminance and poor visibility, they could not use this method at night, so the time period for the study was considered to be from dawn to dusk. The study concluded that the otters allocated 24% of their time to foraging, 59% to resting and 17% to other behaviors.

Walker et al. (2008) based their study design on the methods used by Estes et al. (1986). Scan-sampling was used to determine the activity budget of

translocated sea otters in rocky coastal and subtidal substrate habitats on the Olympic Peninsula in Washington State, an area known to be below equilibrium density. Sampling occurred at 30 min intervals using 10x binoculars and a high-powered spotting scope. The study concluded that sea otters allocated 62% of their time to resting, 20% to grooming, 8% to foraging, 8% to swimming and 2% to other behaviors.

Individual Follows and Instantaneous Sampling

Pearson et al. (2005) conducted their study in Simpson Bay, Alaska, during daytime hours only (0900-1830 h local time). Activities were categorized as foraging, grooming, interacting with other otters, swimming, patrolling, and resting. Pearson et al. (2005) concluded that male otters allocated 30% of their time to foraging, 15% to grooming, 11% to interacting with other otters, 17% to patrolling, 18% to resting, and 9% to swimming (Figure 4b).

Results from This Study

Activity Budget

The same individual follow and instantaneous sampling protocol used by Pearson et al. (2005) was used here, but extended the observations to include the night period. These are two specific forms of focal animal sampling (Altman 1974, Lehner 1996) and should not be confused with group-follows or scan-sampling. In this study, “individual follows” were conducted, whereby observers monitored a single individual regardless of whether it was solitary or in a group, which differs from a “group-follow” where an entire group of animals is monitored

(Mann 1999). In addition, “instantaneous sampling” was conducted, whereby an observer recorded an individual’s behavior at preselected moments in time (i.e. every minute for 31 minutes). In contrast, “scan sampling” involves taking an instantaneous sample of an individual’s behavior at regular intervals before moving on to the next animal, often in a group (Altmann 1974, Mann 1999). As a result, the behavior of a specific animal does not occur during consecutive scans. Scan sampling is valuable for sampling behavior when individual follow observations are not possible, or if the researcher wishes to keep track of group activities. Individual follows and the instantaneous sampling technique is better for determining time budgets, as well as tracking transitional changes in behavior (Altmann 1974, Mann 1999). While this sampling protocol may still slightly underestimate foraging behavior, I think the bias is less than that of the scan sampling method.

This study showed no difference in the mean time spent among the six behaviors in each of the four time periods, although foraging was associated with day and dusk (Figure 5). These results agree with Estes et al. (1986) who reported an afternoon foraging peak that began at approximately 13:00 h, reached a maximum at approximately 16:00-18:00 h and continued until dusk. Male otters in this study allocated 27% of their time (over a 24-h period) to resting, 26% to swimming, 19% to grooming,14% foraging, 9% to patrolling and 5% to interacting with other otters (Figure 4a). Except for Pearson et al. (2005),

previous studies have not attempted or been able to obtain the same level of detailed behavior in male activity budgets over a 24-h period (Table 9).

The allocation of 14% of time to foraging by the male otters in this study was less than observed in most previous studies but considerably higher than reported by Walker et al. 2008 (Table 9). Time budgets of sea otters can be affected by food availability. The low percentage of time allocated to foraging in this study may indicate that food is more abundant in Simpson Bay than other areas in which otters have been studied or that the otter population in Simpson Bay is still below equilibrium density. Where food is relatively abundant, less time is required for feeding, and more time is available for resting or swimming (Garshelis et al. 1986, Bodkin et al. 2007). Previous studies have found that foraging intensity is negatively correlated with sea otter abundance. Otter populations below equilibrium density allocate 15-20% of their time to foraging whereas, those at equilibrium density forage 50-55% of the time (Estes et al. 1986). Simpson Bay was recolonoized by otters over 25 years ago, and the number of otters using it during the summer (June-August) has been stable with ca. 90 adults and subadults and 29 pups (Davis, unpublished observations). Simpson Bay may still be below equilibrium density with 5.6 otters km^{-2} during the peak summer population. This is comparable to a California study (Estes et al. 1986) where the otter population was thought to be at or slightly below equilibrium density with approximately 7.8 otters km^{-2}.

In comparison with male otters in Simpson Bay, female otters with pups invested 21% of their time foraging (Wolt, unpublished data). Although this is 7% higher than the males, it is still at the low end of reported values from other areas, and this leads us to conclude that Simpson Bay may be below equilibrium density. It is reasonable that female otters may forage more than males in order to support their pups. Therefore, the 7% difference in foraging time between males and females can be attributed to provisioning the pup. As a result, the low percentage of time spent foraging by males may have less to due with sampling biases and may indicate that the population is below equilibrium density.

Estimated Field Metabolic Rate (FMR)

The weight-specific FMR for all activities was 686.7 kJ day^{-1} kg^{-1} and the total FMR was 19.04 MJ day^{-1}(Table 8). This level of energy expenditure for sea otters is very similar to predicted values based on allometric regression for FMR of other marine mammals including otariids and phocids (Williams et al. 2004). Yeates et al. (2007) reported an FMR for adult male otters along the California coast to be 15.71 MJ day^{-1}. The difference (21%) in FMR between these two studies resulted from Simpson Bay otters spending more time performing higher energy activities such as swimming and patrolling. The “swimming” category for this energy budget is a combination of both the “patrolling” and “swimming” behaviors from this study’s activity budget. Swimming is usually performed belly up, and can occur at speeds ranging from 0.1-0.5 m sec^{-1}. Patrolling is performed belly down with head raised and can occur at slightly faster speeds

ranging from 0.6-0.8 m sec^{-1} (Williams 1989). In this calculation of FMR, both categories were considered to be surface swimming behaviors and therefore energetically similar. This combined category accounted for 35% of the Simpson Bay activity budget whereas, surface swimming accounted for only 8.5% of the activity budget in Yeates et al. (2007). In addition, grooming accounted for 19% of this activity budget verses 9% of the activity budget described by Yeates et al. (2007). Both grooming and swimming are energetically high-cost behaviors and represent over half of the Simpson Bay male sea otter activity budget. Conversely, foraging and resting are energetically mid-to-low cost behaviors. These activities account for three quarters of the Yeates et al. (2007) budget, while accounting for only 41% of the Simpson Bay sea otter budget.

Foraging accounted for only 14% of the adult male budget, which is low compared to other studies (Table 9). If the male activity budget is revised to reflect the 7% difference in foraging time from the female activity budget (i.e. increase foraging time from 14% to 21%), then the male foraging time would increase to 21% and resting time would decrease to 20%. This would increase the estimated FMR by only 2.5% to 19.50 MJ day^{1}. This low percentage increase in the FMR indicates that 1) any potential bias in the opportunistic focal animal sampling results in relatively minor effects (2.5%) on FMR, and 2) the daily percent time allocated to foraging for male sea otters in Simpson Bay likely ranges between 14-21%. This, in combination with Simpson Bay's stable

summer population density of 5.6 otters km^{-2}, indicates that Simpson Bay may be at or slightly below equilibrium density.

CHAPTER IV

INTERANNUAL ASSESSMENT OF TERRITORY QUALITY FOR MALE SEA OTTERS (*Enhydra lutris*) IN SIMPSON BAY, PRINCE WILLIAM SOUND, ALASKA*

Introduction

Kenyon (1969) originally described territoriality as being weakly expressed in sea otters. However, male territoriality was shown to be a prominent behavior by later studies in California (Vandevere 1970, Loughlin 1980, Jameson 1989, Ralls and Siniff 1990) and Alaska (Calkins and Lent 1975, Garshelis et al. 1986, Gelatt et al. 2002, Pearson and Davis 2005, Bodkin et al. 2007). Prior to their protection under the International Fur Seal Treaty in 1911, the sea otter population in Prince William Sound (PWS), Alaska, was greatly reduced by commercial hunting. The population of sea otters PWS is currently listed as stable or increasing under the Endangered Species Act (Fish and Wildlife Service 2005). Male sea otters are the first to explore new, prey-rich areas (Garshelis et al. 1984) in expanding populations. In the late 1970s, male sea otters began to re-inhabit eastern PWS (Garshelis 1983, Rotterman and Simon-Jackson 1988). Simpson Bay remained exclusively a male area until the 1980s (Garshelis et al. 1984, 1986), but is now used by territorial males, females and pups (Gilkenson 2004, Pearson et al. 2006).

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Sea otters exhibit a form of territoriality, called resource defense polygyny, which is reported for most members of the Family Mustelidae (Calkins and Lent 1975, Loughlin 1980, Garshelis et al. 1984, Jameson 1989, Pearson et al. 2006). Sea otters are sexually segregated when not breeding (Garshelis et al. 1984, Riedman and Estes 1990). Adult males establish territories during the summer and autumn in Alaska (Garshelis et al. 1984, Jameson 1989, Pearson et al. 2006). Female sea otters may be attracted to an area based on a number of factors, including prey availability, protection from waves or wind, accessibility, resting areas, and total area defended from harassment by other males (Garshelis et al. 1984, Pearson et al. 2006). Males will attempt to mate with females that rest or feed in their territories (Loughlin 1980, Riedman and Estes 1990). The peak of breeding occurs during the autumn in PWS, although evidence of copulations has been reported for all seasons (Garshelis et al. 1984).

Maintaining a territory can be energetically expensive for males (Kodric-Brown and Brown 1978; Pearson et. al. 2006). Negative consequences of maintaining a territory may include 1) increased energy expenditure due to courtship, mating and defense activities (e.g., patrolling boundaries); 2) risk of injury or death due to agonistic encounters with conspecifics and predation and, 3) decreased time available for foraging and resting (Clutton-Brock et al. 1988, Apollonio et al. 1989, Vehrencamp et al. 1989, Gosling and Petrie 1990, Isvaran and Jhala 2000, Pearson et al. 2006). However, territoriality can be

beneficial as it increases access to females, thereby enhancing reproductive success (Vehrencamp et al. 1989, Rosser 1992, Isvaran and Jhala 2000, Bro-Jorgensen and Durant 2003, Pearson et al. 2006). Males interact with both single females and females with pups (Pearson and Davis 2005). Males may copulate while guarding females during brief, opportunistic encounters, or during a consortship (Reidman and Estes 1990). Some mature males maintain year-round territories in female areas (Loughlin 1980, Garshelis et al. 1984), but most apparently switch between territorial and non-territorial behavior during the year (Garshelis et al. 1984). It is still undetermined what factors influence a male sea otter's decision to switch between territorial and non-territorial behavior, or what factors maximize the successful impregnation of females.

The Pearson et al. (2006) study of territory costs and benefits determined the territory quality of 10 adult male sea otters in a single season (2003). In this study, territory assessment criteria originally developed by Garshelis et al. (1984), and modified by Pearson et al. (2006) were used to examine the total territory quality of Simpson Bay, Alaska over a four season period (2003 – 2006). It was predicted that the quality of male territories would change from year to year, depending on the number of males holding territories, the size of territories, and whether the male had previously held a territory in the area.

Methods

Study Area

Simpson Bay (ca. 60.6°N Lat., 145.9°W Long.), is located in northeastern Prince William Sound, Alaska. This location was selected as the study site because of its reasonable size, protection from rough seas, and reliable presence of sea otters. It is composed of two arms and has a surface area of *ca.* 21 km^2. The North and West Bays together are 7.5 km long, the East bay is 5 km long, and the entrance is 2.5 km wide. The average depth of the bay is *ca*. 30 m, while the maximum depth is 125 m. The benthos consists of mostly glacial clay, silt, and gravel with some rocky hard reefs (Gilkinson 2004). There are no large-bodied kelps (e.g., *Nereocystis*) that form canopies, but large fronds of sugar kelp (*Laminaria saccharina*) cover the benthos in many areas of the bay from the subtidal to a depth of *ca*. 10 m (Davis, unpublished observations).

For the past eight years, Simpson Bay has been occupied during the summer by an average of 119 $\pm$ 9.3 SD sea otters, including adults and subadults (91 $\pm$ 6.8 SD) and pups (28 $\pm$ 3.8 SD) (Davis, unpub. obs.). Gilkinson (2004) found significant correlations between the distribution of sea otters in Simpson Bay and bathymetry, sediment type and location within the bay (peripheral vs. central). Significantly more sea otters were observed feeding over mud and mud mixed with gravel and sand in shallower areas (< 30 m) along the shore, and significantly more otters were observed resting towards the center of the bay over deeper (*ca*. 30-60 m) water. During the winter, the

number of otters in the bay decreases to *ca*. 50 individuals, although where they disseminate is poorly understood. This research was conducted under a Letter of Confirmation No. MA-043219 from the U.S. Fish and Wildlife Service.

Focal Observations

Field observations of adult male sea otters were conducted during the summers (early May through late August) of 2004-06, and combined with Pearson et al. (2006) data from 2003, using individual follows (Mann 1999) and instantaneous sampling techniques (Altmann 1974, Lehner 1996, Mann 1999, Pearson et al. 2005). The research team conducted surveys from a 6 m skiff, and was composed of a driver, recorder and observer. Simpson Bay was divided into three sections: North Bay, West Bay and East Bay (Figure 1). Each day, one of these areas was selected for conducting observations, and another area was selected as an alternate should logistical problems occur. Boat-based observers determined if an otter was male by observing copulatory behavior, the presence of a penile ridge or testicular bulge (visible through binoculars), or patrolling behavior. Patrolling is a form of locomotion whereby a male swims belly-down with its head out of the water while scanning the surface, presumably for receptive females or other territorial males. Female sea otters primarily swim submerged, or float on their backs, making patrolling a conspicuous male behavior (Pearson et al. 2006).

Individual follows occurred approximately twice a day, during one of four 6-hourly time periods corresponding with astronomical dawn (05:00-11:00), day

(11:00-17:00), dusk (17:00-23:00) and night (23:00-05:00). Each individual follow took place at a distance of not less than 30 m from the target animal in order to minimize the risk of altering the animal's behavior or influence the animal's movement. Opportunistic observations of an individual lasted 31 minutes (minute 0 to minute 30), and instantaneous samples (Altman 1974, Lehner 1996) were taken every 1 minute during which the latitude and longitude were recorded using a Global Positioning System (Garmin, Olathe, KS). Photo-identification was used to identify individual sea otters according to distinctive patterns on the nose or other facial regions (Finerty et al. 2007). At the conclusion of the observation period, the otter was approached to not less than 30 m, and a high-resolution digital image was taken of the head. Images were taken with a Nikon D1H digital camera with an 80-400 mm image-stabilized telephoto lens. Data from individuals that could not be reliably identified or were not sampled ≥ 3 times were dropped from further analysis in this study.

Assessment of Territory Quality

The same four attributes of territory quality used by Pearson et al (2006) as adapted from Garshelis et al (1984) were used in this study: size, shoreline enclosure, accessibility, and prey availability. Ranks of each attribute were coded within a range of 0-2, with higher ranks coding for higher quality (Table 10). Territory size was calculated from minimum convex polygons (Odum and Kuenzler 1955) in ArcMap version 9.2 (Environmental Systems Research Institute, Inc. 2006) using locations obtained during focal observations of

territorial males. Pearson et al (2006) modified the shoreline enclosure attribute criteria from that used by Garshelis et al (1984) because our study site was a bay on the mainland rather than coves on an island (Table 10). Shoreline enclosure on 2 sides was scored as high quality, as opposed to the "3 side" criteria defined by Garshelis et al (1984). Accessibility was ranked based on the number of entrances blocked by the territories of other males (Table 10). A territory located at the "dead end" of the arm of a bay had a lower accessibility rank than one located at the "mouth of the arm". Males tended to intercept females entering at the "mouth of the arm".

Because the distribution and abundance of benthic macroinvertebrates has not been determined for Simpson Bay (Gilkinson 2004), prey availability was estimated using an approach similar to that of Garshelis et al (1984) and Pearson et al (2006). Pearson et al (2006) assigned a score for "food availability" (Table 10) based on the number of females observed feeding within each territory. In this study, female observations that were gathered by a concurrent study (Wolt et al. in prep) were used. While making observations of female behavior, Wolt et al. (in prep.) also recorded the GPS coordinate sets of each feeding female encountered. Those coordinate sets were then plotted in ArcMap to estimate the number of feeding females in each territory. The number of feeding females from 2004-2006 were similar to those recorded in 2003 by Person et al (2006). It was assumed that female sea otters would aggregate where food resources were plentiful, being "better samplers" than

Table 10. Adaptation of criteria for assessing relative quality of sea otter (*Enhydra lutris*) territories in Prince William Sound, Alaska (Pearson et al., 2006)

Attribute	Adapted criteria (Pearson et al. 2006)	Original criteria (Garshelis et al. 1984)	Rank value
Size (km^2)	>1.0	>0.3	2
	0.5-1.0	0.15-0.3	1
	<0.5	<0.15	0
Shoreline enclosure	Land on two sides	Land on three sides	2
	Land on one side	Land on two sides	1
	Mainly open	Mainly open	0
Accessibility	Entrance(s) not blocked by another territory	Entrance(s) not adjacent to another territory	2
	Entrance(s) partly blocked by another territory	Entrance(s) partly blocked by another territory	1
	Entrance(s) mostly blocked by another territory	Entrance(s) totally blocked by another territory	0
Prey availability	Number of females feeding in territory divided by 10*	Number of females feeding in a territory divided by 20** (values ranged from 0 to 2.1)	NA

*The number of females we observed was half as many as that observed by Garshelis et al. (1984)
** The prey availability attribute was divided by 20 to scale with the other 3 attributes

researchers (Garshelis et al. 1984, Pearson et al. 2006). It was also assumed that the number of females feeding within each territory was a good indication of prey availability because the foraging success rate was 89% in Simpson Bay during the summer of 2003 (Wolt et al. in prep).

Sea otters have great potential to be influenced by their habitat due to their diet of benthic invertebrates which requires them to dive through the entire water column and excavate bottom sediments. Thus, as another way to describe territories, sediment data collected by Gilkinson (2004) was used. Gilkinson (2004) determined the habitat characteristics of Simpson Bay by measuring water depth and taking sediment samples with an Eckman grab, as well as visually examining the seafloor with a black-and-white video camera at 198 separate data stations throughout the bay. Sediment type was then classified in gravel-sand-mud categories based on grain size distributions of each sediment sample. Sediment categories were recorded as gravel, mixed gravel (including sandy gravel and muddy gravel), sand, mixed sand (including gravelly sand and muddy sand), mud, or mixed mud (including sandy mud and gravelly mud). In the present study, maps of sea otter territories were overlaid on Gilkinson's bathymetry and sediment type maps to determine the maximum depth and bottom type for each territory.

Data Analysis

A summary quality score was calculated for each territory because the four attributes of quality were intercorrelated (Table 11). For example, territories

Table 11. Variation in territorial attributes (Table 1) for territorial male sea otters in Simpson Bay, Alaska during the summers of 2003-2006

	Territorial attribute				Quality Score (PCA)	
Male ID (year)	Size	Shoreline enclosure	Accessibility	Prey availability	Component 1*	Component 2**
Ch (2003)	2	1	1	1.3	1.96	0.10
Je (2003)	2	2	1	0.7	1.72	1.37
Ot (2003)	2	2	1	0.5	1.62	-0.42
Li (2003)	2	0	1	0.2	1.30	0.74
Wi (2003)	1	1	2	0.1	0.83	0.74
Os (2003)	1	1	0	0.1	0.69	-0.52
Cu (2003)	1	0	1	0.1	0.68	0.68
Jb (2003)	0	1	1	0	0.15	0.06
De (2003)	0	0	2	0	0.14	1.26
Ha (2003)	0	0	2	0	0.14	1.26
Ch (2004)	2	1	1	0.7	1.64	0.14
Cu (2004)	2	1	1	0.4	1.48	0.16
Em (2004)	2	1	1	0.3	1.43	0.16
Wi (2004)	1	1	1	0.3	0.87	0.10
Ot (2004)	1	0	1	0.4	0.84	0.67
Td (2004)	0	1	0	0.5	0.35	-0.60
Bj (2004)	0	1	0	0.1	0.13	-0.58
Mu (2005)	2	1	2	0.4	1.55	0.79
Ja (2005)	1	0	2	0	0.70	1.32
Be (2005)	0	1	1	0.2	0.26	0.05
Pu (2005)	0	1	1	0	0.15	0.06
Ni (2006)	2	0	1	1.1	1.77	0.68
Dr (2006)	2	1	1	0.6	1.59	0.14

Table 11. Continued

Male ID (year)	Territorial attribute				Quality Score (PCA)	
	Size	Shoreline enclosure	Accessibility	Prey availability	Component 1*	Component 2**
Ri (2006)	1	1	1	0.8	1.13	0.07
Gr (2006)	1	0	2	0.6	1.02	1.28
Pe (2006)	1	0	1	0.5	0.90	0.66
Be (2006)	0	1	1	0.1	0.20	0.05
Qu (2006)	0	1	1	0.1	0.20	0.05

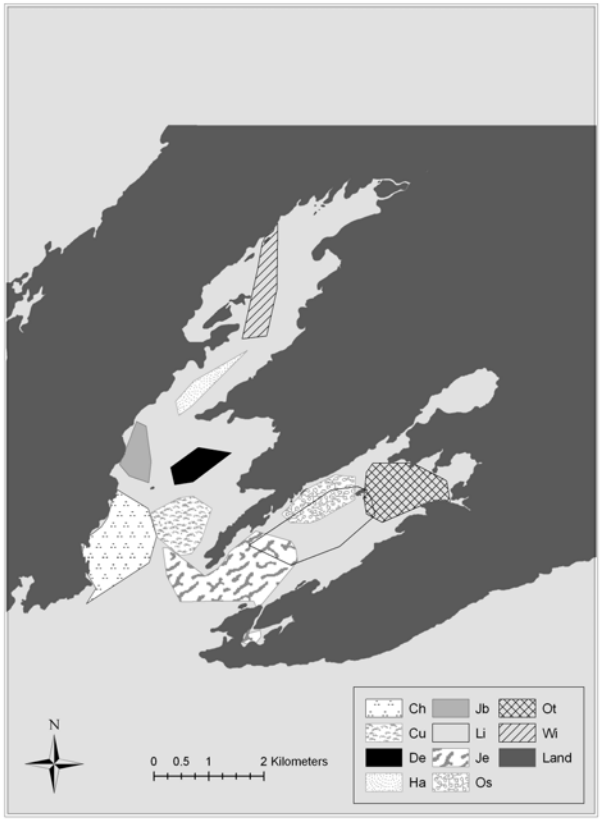
* Component explaining 43% of total variance; used to calculate summary scores; weighted to size and prey availability

** Component explaining additional 32% of total variance; weighted to shoreline enclosure and accessibility

located in the heads of the bays were ranked low for accessibility, and high for shoreline enclosure. In addition, these territories also tended to be smaller in size than those territories located at the mouths of each bay (Pearson et al. 2006). Summary scores for territories found in 2004-2006 were calculated following the procedure of Pearson et al (2006) and Garshelis et al (1984), which allowed the 2003 dataset to be combined with the 2004-2006 dataset. A linear combination of variables was selected to best describe the orthogonal variation in the data. Principle components analysis (PCA) was used to transform the set of intercorrelated variables into a set of uncorrelated linear combinations of these variables (Dunteman 1989, Stevens 1992, Bryant and Yarnold 2003).

Territory overlap was assessed by comparing the minimum convex polygons of each individual within each year (Figure 7a-d). To understand the relationship between territory overlap and physical interactions between males, ad libitum sampling (Altmann 1974) was conducted to record all instances of aggression between males.

Analysis of Covariance (ANCOVA) was conducted to test the influence of number of territorial males (as the covariate) on: (*i*) territory quality among individual males, and (*ii*) territory size among individual males. Univariate as well as multivariate analysis of variance (ANOVA and MANOVA, respectively) was used to test relationships between the following: (*iii*) territory quality and otter category (males that held a territory in consecutive years versus males that held



a) 2003

b) 2004

Figure 7. Territory of male sea otters (Enhydra lutris) in Simpson Bay, Alaska during the summers of a)2003, b) 2004, c)2005 and d) 2006

c) 2005

d) 2006

Figure 7. Continued

a territory in only one year), (*iv*) territory quality and year, (*v*) territory size and otter category, and (*vi*) territory size and year. All statistical analyses were calculated using *SPSS version 15* statistical software (SPSS Inc. 2006). The alpha level for all tests was set at 0.05.

Results

Over the four year period, male territories in Simpson Bay had an average size of 0.95 km^2 ± 0.10 SD (range 0.35-2.57 km^2) and an average maximum depth of 56 m ± 7.40 SD (range 30 – 90 m). Territories occupied 48% of Simpson Bay in 2003, 35% in 2004, 16% in 2005 and 28% in 2006. In total, 13.1 km^2 (62.5%) of Simpson Bay was occupied at least once by a territory during the four year study (Figure 8), and 7.9 km^2 (37.5%) was never occupied by a territory. In addition, 23% of the total area occupied by individual territories was over sand or mixed sand sediment types, 28% was over gravel or mixed gravel, and 49% was over mud or mixed mud.

Individual territories in Simpson Bay overlapped by 6.9% in 2003, 2.9% in 2004, 0% in 2005, and 14.4% in 2006 (Figure 7a-d). Males Ch, Cu, Ot, and Wi held territories in 2003 and 2004, and their respective territories overlapped by 26.6-34.2% between years (Figure 9a-d). Between 2005 and 2006, the territory of male Be overlapped by 16.4% between years (Figure 9e).

Recognition methods involved boat-based observations, and therefore the potential for observer effects on sea otter movements may have slightly increased. However, the 30 m minimum distance between the boat and target

Figure 8. Area of Simpson Bay, Alaska that was covered by a male sea otter territory at least once from 2003 to 2006

a) Male Ch territory 2003-04 (28.5% overlap)

b) Male Cu territory 2003-04 (34.2% overlap)

Figure 9. Territory locations for repeat territory holders between years a) Ch b) Cu c) Ot d) Wi and e) Be

c) Male Ot territory 2003-04 (26.6% overlap)

d) Male Wi territory 2003-04 (28.9% overlap)

Figure 9. Continued

e) Male Be territory 2005-06 (16.4% overlap)

Figure 9. Continued

animal, as permitted by the US Fish and Wildlife Service, was strictly adhered to in order to minimize the risk of altering the animal's behavior or movement.

Territory Quality

The first principle component of the PCA (eigenvalue of 1.73) accounted for 43% of the total variance among the four attributes of territory quality and was used to calculate the summary scores for each territory based on the weights of the coefficients for each variable:

$$y = 0.56_{size} + 0.08_{enclosure} + 0.07_{access} + 0.53_{prey}$$

Large territories with many prey resources scored high for this index. Territory quality scores ranged from 0.14 to 1.96 (0.9 $\pm$ 0.61 SD) (Table 11). For example, male Ch held the highest quality territory in 2003, located near the mouth of West Bay whereas, males De and Ha (also in 2003) defended the lowest quality territories, located in the northern portions of the West Bay (Figure 7a).

The second principle component, explaining an additional 32% of the total variance among attributes of quality, was negatively related to the degree of enclosure and positively related to the degree of accessibility ($y = 0.06_{size} - 0.57_{enclosure} + 0.63_{access} - 0.06_{prey}$). Therefore, highly enclosed territories that were primarily obstructed by other territories scored low for this index. High quality territories had (i) large areas, (ii) some feeding sites for females, (iii)

moderate to little shoreline enclosure, and (iv) more entrances away from other territories (Table 11).

Territory Correlations

The ANCOVA showed that the total number of males holding a territory in Simpson Bay had no significant effect on the size (p = 0.845) or quality (p = 0.804) of the territories. The ANCOVA also found no interaction (year*total otters) effect on the size (*p* = 0.423) or quality (*p* = 0.177) of the territories. A two-way ANOVA showed that neither year (p = 0.639) nor otter category (p = 0.804) had a significant effect on the quality of the territories over the four years. In addition, there was no significant interaction (year*individual otter) effect on the territory qualities (p = 0.177). The MANOVA also showed no significant effect of year (p = 0.898), individual otter (p = 0.969), or their interaction (p = 0.166), on the quality or size of territories of either repeat or non-repeat territory holders over the four years.

Male-Male Interactions

Two physically aggressive male/male interactions were observed in Simpson Bay during the four year period. In 2003, males Li and Ot held adjacent territories in the East Bay. On several occasions, male Ot invaded male Li's territory only to be chased out with no physical interaction. However, on July 19, male Ot encroached upon male Li's territory. Male Li was observed patrolling its territory when it came upon male Ot, and a physically aggressive encounter ensued. Both males began lunging, hissing, biting and scratching

each other. The physical interaction lasted approximately three minutes. Male Li then chased male Ot back to its adjacent territory but abruptly stopped the chase at what appeared to be its territory boundary, while male Ot continued swimming and porpoising farther into its own territory.

The displacement of one territorial male by another was witnessed in 2004. Male Ch was displaced by a transient male (Ro) for approximately 12 days. On August 13, male Ch was observed in a physically aggressive encounter (biting and scratching) with an unidentifiable male (later presumed to be transient male Ro). On August 15, transient male Ro was observed in male Ch's territory. During this time, male Ch was not seen in any part of the study area. However, on August 25, male Ch was observed resting back in its original territory. On August 28, transient male Ro was observed and monitored patrolling the outskirts of male Ch's territory, then leaving the study site. Transient male Ro was only observed twice and was therefore excluded from further analysis in this study.

Discussion

The results of this study support a common finding: during 2003-2006, the quality and size of territories in Simpson Bay were not significantly different among years and not significantly influenced by the total number of otters holding territories, or whether or not an individual otter held a territory in the area during consecutive years.

Territory Quality

The importance of the four major territorial attributes (size, shoreline enclosure, accessibility and prey availability) to overall territory quality was similar between this study, Pearson et al. (2006), and Garshelis et al. (1984). In each study, size was the most important territory quality, followed by prey availability. However, Pearson et al. (2006) found that higher quality territories had more entrances obstructed by other territories while this study and that of Garshelis et al. (1984) found the opposite. Territories with the higher quality scores were those that had boundaries away from other territories, moderate to little shoreline enclosure, large areas and some feeding sites for females.

On average, Simpson Bay territories had an area of 0.95 km^2 $\pm$ 0.1 SD (range 0.35-2.57 km^2). Previous studies have reported smaller territories. For example, Garshelis et al. (1984) conducted a study in Prince William Sound at Gibbon Anchorage from 1975-84 and found the average male territory area to be approximately 0.23 km^2 (range 0.04-0.50 km^2). Jameson (1989) conducted a study from 1978-82 along the California coast from Santa Cruz to Pismo Beach and found the average male territory area to be approximately 0.36 km^2 (range 0.23-0.62 km^2). Larger territory areas in Simpson Bay may result, in part, from its size and location. Gibbon Anchorage is approximately 3.5 km^2 in area and is considered to be a partially enclosed region (Garshelis et al. 1984). Jameson (1989) conducted his study on over 200 km of the California coastline which contains few enclosed areas for protection from rough seas. Simpson Bay,

which is located inside of PWS and protected from sea conditions in the Gulf of Alaska, is 21 km^2 in area and is almost entirely enclosed (except for the 2.5 km wide entrance to the bay). This offers much protection from rough seas, thus making it easier for males to patrol larger areas. However, both Gibbon Anchorage and the California coast have been occupied by sea otters for longer periods of time than Simpson Bay. It is possible that there is more competition for territories in those areas. It is also possible that other factors that are not yet fully understood, such as food availability, might affect territory size.

Much the area in Simpson Bay that was unoccupied by territories was located at the mouth or head of each portion of the bay. The mouths of West and East Bays, while having no shoreline enclosure (a positive attribute), are also located over deeper (60 - 125m) water. Deep water may limit the number of feeding sites available (Gilkinson 2004). In contrast, the heads of North and East Bays were very shallow and often included areas exposed at low tide. Because Simpson Bay has semidiurnal tides, this would considerably decrease the territory size twice during each 24 hr period, depending on the time of the month. In addition, entrances to these areas were often blocked by other territories, which this study has shown to be an undesirable territory attribute.

Territory Overlap and Physical Interactions

There was little territory overlap in Simpson Bay, indicating that male sea otters may avoid conflict by maintaining non-overlapping territories. As in other studies (Calkins and Lent 1975, Loughlin 1980, Garshelis et al. 1984), territorial

trespassing by other males, whether resident or transient, was not frequently observed, and therefore very little male/male aggressive behavior was observed. In the present study, only two aggressive interactions between males involved physical contact, and only one instance of territory displacement occurred. Most trespassers were deterred from entering a territory without physical interaction with the territory holder. Aggressive vocalizations such as hissing or growling, chasing, or simply the territory holder's presence in the area were often enough to discourage a trespasser from invading a territory.

Site Fidelity and Repeat Territory Holders

Fidelity by individuals to an area over multiple years provides strong evidence of stable resources and social systems (Powell 2001), as well as insight into how animals use an area over time (Kernohan et al. 2001). However, some changes in space utilization over the course of multiple years may occur because of competition for resources (Powell 2001). In the present study, 5 of 23 territorial male sea otters held a territory for two consecutive years. Territory overlap for a given male between years ranged from 16.4 to 34.2%. Although some shifting occurred, male sea otters occupied the same territory during consecutive years. This indicates stability of resources as well as competition between males for those resources.

In previous studies, the time that an adult male sea otter held a territory ranged from 1-9 years (Garshelis et al. 1984, Jameson 1989). Garshelis et al. (1984) captured otters in floating nets, marked them with colored tags, and then

monitored their movements with binoculars and spotting scopes. Eight tagged males held territories during the breeding season during each of two consecutive years, and one male held a territory for at least nine consecutive years (Garshelis et al. 1984).

As in the Garshelis study, Jameson (1989) captured otters and marked them with colored tags and then monitored them during daily surveys. Two otters maintained the same territory for five consecutive years, two for six years, and one for seven years. No tagged males changed territories within the study area, and it was noted that males frequently rested within a few meters of the same location during each survey (Jameson 1989).

Site fidelity studies have been conducted on both aquatic and terrestrial animals including other mustelids (river otters [*Lontra Canadensis*]; Gorman et al. 2006), pinnipeds (Northern fur seals [*Callorhinus ursinus*]; Kiyota 2005), and ungulates (guanacos [*Lama guanicoe*]; Young and Franklin 2004).

River otters exhibit strong annual site fidelity by both males and females. Gorman et al. (2006) conducted a two year study that showed male river otters used 74% of their year 1 home range in year 2, while females home ranges overlapped by 75% between years. As with sea otters, some shifting of river otter home ranges occurred between years, but none of the river otters completely abandoned or relocated their home ranges during the study (Gorman et al. 2006).

Kiyota (2005) investigated territory acquisition and mating success of male northern fur seals on St. Paul Island (Pribilof Islands), Alaska from 1993-99. Adult female fur seals arrive at the breeding colony in early summer and tend to aggregate in “central breeding areas” (Kiyota 2005). Similar to adult male sea otters, one attribute for a high quality territory for an adult male fur seal is the spatial and temporal concentration of receptive females. Many prime male fur seals initiated their territory tenure in early summer (May or June). As with adult male sea otters, once adult male northern fur seals acquired breeding territories, they displayed strong tendencies to return to the same locations during the following breeding seasons (Kiyota 2005). Male fur seals can hold a territory for one to five years, with an average of two years (Kiyota 2005).

Southern Chilean guanacos establish territories in the spring to prepare for the summer mating season (Young and Franklin 2004). Adult males are found in one of three social groups (Franklin 1982, Young and Franklin 2004). Similar to territorial male sea otters, solitary male guanacos establish non-overlapping territories for an average of two years (range 1-5 years). Family groups include a territorial male, several adult females, some yearlings and other young. Lastly, male groups are composed of non-territorial males, immature males and old or injured males and occur in distinct areas (Young and Franklin 2004) similar to rafts of non-breeding male sea otters (Kenyon 1969, Garshelis et al. 1984, Pearson et al. 2006).

Bathymetry and Sediment Type

Gilkinson (2004) observed that significantly more otters were feeding over mud and mixed mud sediments. The present study found that nearly half (49%) of the total area in Simpson Bay covered by territories from 2003 to 2006 consisted of mud or mixed mud sediments. This study has shown the availability of feeding sites to be a favorable territory attribute.

Sample Size

Sample sizes in previous studies of territorial males have been small, ranging from 2-12 individuals (Jameson 1989, Pearson et al. 2006). Pearson et al. (2006) concluded that because of the physiography of Simpson Bay, the sample size was not likely to exceed 10 territorial males in any one year. This study supports that conclusion. Simpson Bay supported an average of 7 $\pm$ 2.4 SD territorial males each year. At any one time from 2003-06, there was a maximum of two territories in the North Bay and four territories in either the West or East Bays (Figure 7).

The results of this study indicated that the best male territories in Simpson Bay had large areas, moderate shoreline enclosure, were not blocked other male territories, and had food resources to attract foraging females. However, there are probably other contributing variables to territory quality that have yet to be identified, such as the number of females that a male impregnates in a given season. This type of assessment will require new

research techniques for tracking and monitoring the long term movements and behavior of sea otters and determining when impregnation occurs.

CHAPTER V

SUMMARY

Photo Identification

The Sea Otter Nose Matching Program (*SONMaP*) was the first computerized individual identification method developed for use with sea otters. Digital images of sea otters were taken from June to August of 2002 and 2003. With images of high quality and distinctiveness, the performance of the user-dependent *SONMaP* was similar to that of other matching software designed and tested for use with cetaceans. However, the quality of the raw and normalized images and the distinctiveness of the nose scars greatly influenced the accuracy of the *SONMaP* program. In this study, *SONMaP* performed well enough to provide significant assistance in the process of photo-identification by reducing the time needed to match sea otters within a catalog by about two-thirds (67%), and can be used in the field.

Attempting to visually identify a sea otter image against a catalog of over 1,600 images without computer assistance can be very overwhelming and time-consuming for the researcher. The reduction in time allows the researcher to evaluate images from very large catalogs in less than half the time needed for identification without computer assistance. The capability to evaluate such large catalogs provides the ability to identify individual otters between years and the possibility of tracking some changes to individual nose scars. Until more information is obtained on the stability of sea otter nose scars, *SONMaP* may be

most useful for identifying sea otters on an intra-annual basis. However, it may be possible to identify some sea otters, especially adult males, over longer periods of time.

Activity Pattern and Field Metabolic Rate

Opportunistic individual follows and instantaneous sampling techniques were used to determine the daily activity budgets and estimate the Field Metabolic Rate (FMR) of adult male sea otters during the summer months (May to August) of 2005 and 2006. These data collection techniques were also used to gather data pertaining to the territory quality of adult male sea otters in Simpson Bay, during the summer months of 2003 to 2006.

A study by Pearson and Davis (2005) was the first to create an activity budget for adult male sea otters in Simpson Bay. However, the study examined only daytime behavior. A 24-h activity budget had never before been attempted in Simpson Bay. Over a 24-h period, adult males allocated 35% of their time to swimming and patrolling, 27% to resting, 19% to grooming, 14% to foraging and 5% to interacting with other otters. Interacting and resting behaviors were positively associated with the dawn time period. Grooming, while not significant, also tended to be positively associated with the dawn time period. In addition, the combined activity of swimming and patrolling (called swimming) accounted for the greatest percentage (43.3%) of energy expended each day, followed by grooming (23.2%), resting (15.2%), feeding (13.1%) and other (5.1%).

The 24-h budget provides a better understanding of sea otter behavior. Other studies in Alaska have developed 24-h activity budgets, however, many have used scan sampling, or electronic means such as radio telemetry or time-depth recorders. A 24-h activity budget developed by Garshelis et al. (1986) in PWS used radio tags attached to both adult male and female sea otters. This study was able to identify only three specific behaviors from the radio signals: resting, swimming, and foraging. Gellatt et al. (2002) combined scan sampling techniques with radio telemetry to develop a 24-h activity budget for adult male and female sea otters in Amchitka, Alaska. Nine different behavioral categories were recognized in the study including, feeding, resting, grooming, swimming, interacting, stealing of food, hauled out, active unknown (other) and unknown (lost signal). Bodkin et al. (2007) used time-depth recorders to develop a 24-h activity budget for adult male sea otters in Cross Sound, Alaska. Five behavioral categories were recognized by the study including, resting, feeding, swimming, grooming and interacting.

This study recognized 6 specific behavioral categories (excluding “other” or “unknown” behaviors) over a 24-h period for adult male sea otters only. In addition, the individual follows used in this study were able to track the otters’ behavioral transitions. These fine points allow this study to be described as one of the most detailed activity budgets ever attempted for adult male sea otters.

Yeates et al. (2007) was the first to develop an energy budget for adult male sea otters. In that study, a daytime activity budget was developed from

radiotelemetry data collected from male sea otters in California. The open-flow respirometry results were applied to the daytime activity budget, thus creating a daytime energy budget.

This study was the first to attempt the development of a 24-h energy budget for sea otters, and showed that energy expenditure for feeding and swimming had a more positive association with the day time period, whereas energy expenditure for grooming and resting showed a more positive association with the dawn time period. Although individual follows and instantaneous sampling may underestimate the percentage of time spent foraging, the estimated FMR (19.04 MJ day^{-1}) was relatively insensitive (2.5% difference) to changes in the percentage of time spent foraging which likely ranged from 14-21%. Even if male sea otters allocated 21% of their time foraging, this is less than observed in most previous studies and, in conjunction with a stable summer density of 5.6 otters km^{-2}, indicates that Simpson Bay may be at or slightly below equilibrium density.

More information is needed on adult male sea otter behavior and energy expenditure throughout the remainder of the year. Year-round observations would not only improve our understanding of adult male sea otter summer behavior, but also provide insights to sea otter behavior during cooler seasons. Comparison of activity budgets between seasons would lead to a better understanding of and more specific calculation of adult male sea otter field metabolic rates.

Another important “next step” would be to gain a better understanding of the low (14%) foraging time found during this study. Do male sea otter foraging budgets change with time of year? Is more or less foraging done during cooler seasons? In this study, foraging was associated with the day and dusk time periods. Does this change in colder seasons when the light levels change drastically in Alaska (as compared to California)? Further observation will yield important information regarding any changes to the foraging time budget due to season, month, and/or time of day.

Improvements to the FMR calculations may be done by finding the caloric content of specific prey items and average intake of those items by sea otters in Simpson Bay. In this study, the primary prey item observed was clams. Do otters switch to different primary prey items with season, and thereby change their caloric intake, as well as energy expenditure? All of this information could provide further insight regarding the productivity of Simpson Bay.

Territory

A combination of four variables (size, shoreline enclosure, accessibility, and the number of foraging females observed) was used to characterize the quality of male sea otter territories. These four attributes included both physical aspects of their habitat as well as variables related to female choice for residing in an area. Principle Components Analysis (PCA) was used to calculate summary scores for each individual territory. The results indicated that the best male territories in Simpson Bay had large areas (average size was 0.95 km^2 $\pm$

0.10 SD), moderate to little shoreline enclosure, had a high degree of accessibility (were not blocked by other male territories), and had food resources to attract foraging females (49% of territorial areas were over sediments shown to attract feeding otters: mud and mixed mud). Multivariate and Univariate Analysis of Variance (MANOVA and ANOVA) concluded that the quality and size of territories in Simpson Bay were not significantly different among years and not significantly influenced by the total number of otters holding territories, or whether or not an individual otter held a territory in the area during consecutive years.

Pearson et al. (2006) was the first to study territory quality in Simpson Bay. That study covered a single year population of territorial males in the study area. This study was the first multi-year territory quality study done in Simpson Bay. At 4 years in duration (including data from Pearson et al. 2006), this study was able to compare territory quality inter- as well as intra-annually, and allowed the observation of the areas of the bay that were favored for territories between years.

In addition, this study was the first to compare the territory quality of five territorial males that held their territories for 2 consecutive years. Each of these five territories had only minor shifting in location between each year of occupancy. During this 4 year study, only 2 ad libitum (Altmann 1974) observations of aggressive physical interactions between males were

encountered. All of these data further support that sea otters exhibit site fidelity to territorial areas.

More information is needed on territory preference and territory quality throughout the remainder of the year. Some mature males maintain year-round territories in female areas (Loughlin 1980, Garshelis et al. 1984), but most apparently switch between territorial and non-territorial behavior during the year (Garshelis et al. 1984). It is still undetermined what factors influence a male sea otter's decision to switch between territorial and non-territorial behavior. It is also still undetermined if a territorial male otter population is present in Simpson Bay during the winter season. If a population does exist, an interesting line of research may include a comparison of territory quality during winter months to territory quality in the summer months. If a population does not exist, then another area of study may cover the average time of year that the otters vacate Simpson Bay, and the average time of repopulation. This information would provide a greater understanding of the overall quality and attractiveness of Simpson Bay, as well as present additional insight to sea otter territoriality and site fidelity as compared between Alaska and California sea otters.

There are probably a number of other variables that contribute to territory quality including the number of females that a male impregnates in a given season. Until new technology is developed to determine the exact time of sea otter impregnation, a future "step" in this research is to begin cataloging each male's copulatory encounters and identifying each female. Do the same

females remain in the same male's territory for the duration of the breeding season, or do the females opportunistically switch to a more "attractive" territory?

This study has provided important information to extend our understanding of sea otter habitats and behavioral ecology. However, science is a never-ending progression where a single answer can lead to multitudes of additional questions. It is important that the photo-identification, behavioral, and territorial research continues on the sea otter population in Simpson Bay. These continuing, time-series studies will be essential to assessing long term patterns or shifts in sea otter population demographics, behavior, and territory quality.

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VITA

Name:	Shannon Elizabeth Finerty
Address:	Laboratory for Aquatic Animal Performance Texas A&M University 5007 Avenue U Galveston, TX 77551
Email Address:	shannonfinerty@yahoo.com
Education:	B.S., Biology, Magna Cum Laude, Saint Joseph's College, 2003 Ph.D., Wildlife and Fisheries Sciences, Texas A&M University, 2010